Genetic Improvement of Tomato

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General Importance

The tomato is a universally known vegetable and is one of the most widely grown. Its popularity is due in large part to its versatility and the variety it lends to the human diet. With the exception of potato (often classified as starchy staple), tomato leads all other vegetables in total production volume (Table 1).

Nutritionally, tomato may not rank high in concentrations of essential nutrients, yet, because of its popularity and diverse uses, it is an important alleviant of nutritional deficiency. In the United States, for example, tomato ranks only 13th and 16th among the main vegetables and fruits as vitamins C and A sources, respectively. However, it outranks all others in terms of total contribution of vitamins and minerals to the diet mainly on account of the high consumption volume for tomatoes, both in fresh and processed forms. In its own right, tomatoes have become almost a dietary staple.

Table 1. World production (x 1000 tons) of selected vegetables (1980 & 1987)

Crop	1980	1987
Tomato	50, 153	61, 363
Potato	225, 718	285, 009
Cabbages	35, 139	38, 132
Green beans	2, 428	3, 042
Peppers	6, 888	8, 740
Onions	19, 410	25, 282

Source: FAO Production Yearbook. 1980 & 1987.

Rick (1978) states "it is hard to realize now, when tomato is highly popular not only as a food in its own right but also as an ingredient of soups, sauces (including the ubiquitous catsup) and drinks, that as recently as 1900 it was widely avoided in the belief that it was poisonous because of its known relation to the nightshades and other toxic members of the nightshade family". Indeed, the story of tomato's transformation from an exotic fruit to a popular dietary item and a major commodity of commerce the world over is one of the most fascinating events in the saga of crop domestication. Its popularity is phenomenal and total production continues to rise in all four continents (Table 2).

Table 2. Trends in tomato production in different regions of the world

Region	Area ('000 ha) 1987	% Change (vs 1980)	Production ('000 tons) 1987	% Change (vs 1980)
Asia	832	+18.5	15,382	+29.8
Europe	448	-5.7	16,147	+10.8
North/Central America	307	+0.6	11,341	+23.3
South America	143	+10.9	3,718	+26.2
Africa	478	+27.8	7,240	+41.4

History of Domestication and Cultivation

All the cultivated forms of the tomato belong to *Lycopersicon esculentum*. It is generally accepted that the cultivated tomato originated from the New World (the Americas) since all related species of tomato are native to the Andean region now encompassed by the parts of Bolivia, Chile, Colombia, Ecuador and Peru. From these native habitats, tomato was taken to Europe soon after the discovery of the New World, very likely in already a fairly advanced stage of domestication. Writings as early as 1544 such as that of Mattiolus in Venice described a golden-fruited plant which was almost surely *L. esculentum*. A red-fruited form was described in a later writing. Furthermore, woodcuts from the early herbals clearly showed that the first types of tomatoes cultivated in Europe bore large fruits, typical of the tomato we know today. In contrast, all related wild species bear small fruits.

Evidence from the diversity of cultivated types and culinary uses and from the abundance of native names for the tomato fruit all suggest that tomato was originally domesticated in Mexico (Jenkins 1984). Its most likely ancestor is the wild cherry tomato (*L. esculentum* var. *cerasiforme*) which is spontaneous throughout the tropical and subtropical America and has later spread throughout the tropics of the Old World. Selection over many generations presumably led to increased fruit size and higher ratio of fruit weight to seed content that are typical of the modern-day tomato. The name "tomato" comes from Nahuatl language of Mexico and variants of this name have followed the tomato in its spread throughout the world (Heiser 1969).

Biosystematics of the Genus *Lycopersicon*

The tomato is a member of the Solanaceae or the nightshade family, a collection of some 1500 tropical and subtropical species probably originating in Central and South America. It is an important family as a food source (e.g. tomato and potato) although many of its members are characterized by relatively high concentrations of glycoalkaloid such as solanine, nicotine, scopolamine, atropine, tomatine, etc. The predominant alkaloid in the tomato is tomatine, which is at its highest concentrations in the foliage and the green fruit and is degraded to inert compounds on ripening.

Within the family Solanaceae, the genus *Lycopersicon* is a relatively small collection of species that are normally subdivided into two groups, the *Eulycopersicon* and the *Eriopersicon*. Fruits of the *Eulycopersicon* are usually red or yellow in color when ripe. The cultivated tomato, *Lycopersicon esculentum*, belongs to this group. In contrast, fruits of the *Eriopersicon* remain green or purple green throughout their development. At present, nine species are recognized as distinct entities within the genus *Lycopersicon* (Table 3). The first generally accepted description of several species of tomato, including the common one, was made by Miller in 1768; hence, various texts refer to the Latin name of tomato as *L. esculentum* Mill. in honor of Miller.

Genetic Diversity

Research on the nature of genetic diversity of *L. esculentum* has facilitated the understanding of the evolution of the cultivated forms and their further genetic improvement. The general agreement from such studies is that the cultivated and wild forms of *L. esculentum* are remarkably homogeneous (disregarding recent hybridizations with accessions from the native region) outside their native region of western South America. In contrast, more variation is present in the native region both within and between accessions. Several factors have been postulated to account for these differences: interbreeding with wild species in the native region; greater activity of insect pollinators promoting more outcrossing; effects of artificial selection; longer period of existence in the native region allowing the accumulation of more variants; and, genetic drift in the long migration from South America through Central America and Mexico coupled with natural selection for limited number of successful genotypes.

All members of the genus *Lycopersicon* are annual or short-lived perennial herbaceous diploids with a somatic chromosome number of 24. The cultivated tomato is a perennial plant normally grown as an annual. The genus as a whole tolerates a wide range of climatic conditions. For instance, *L. pennellii* (formerly *Solanum pennellii)* survives in very dry, rolling hills of western Peru whereas *L. cheesmanii* has been observed to grow in salt-laden atmospheres, just a few meters above the high water mark of the northwestern shores of the Galapagos Islands (Rick 1977).

In general, the relatives of the cultivated tomato have proven to be invaluable sources of desirable genes for further genetic improvement (Rick 1967; Rick 1981; Rick 1986). Examples of useful characters derived from the wild relatives of the tomato are as follows: jointlessness and salt tolerance from *L. cheesemanii*; high soluble solids from *L. chmielewskii*; resistance to Botrytis mold, Septoria leafspot and insect pests from *L. hirsutum*; TMV and rootknot nematode resistance from *L. peruvianum*; resistance to curly top virus from *L. chilense*; resistance to Fusarium wilt, gray leafspot, Cladosporium leafmold and spotted wilt virus from *L. pimpinellifolium*; and resistance to anthracnose, Alternaria collar rot, and Verticillium wilt from *L. esculentum* var *cerasiforme*.

The utilization of the above traits in improving cultivated tomato has been made possible by the ease with which interspecific crosses within and between groups is made (Table 4). Hybridization within the Group *Eulycopersicon* (red-fruited forms) show few, if any, barriers to gene exchange. The group is also crossable with members of the Group *Eriopersicon* (green-fruited forms) but in some cases, only when the latter functions as the pollen parents. This condition is termed "unilateral incompatibility". Where such incompatibility exists, the interspecific F_1 hybrid will hybridize with the cultivated *L. esculentum* only as a pollen par

ent; in crosses to the wild species, the F_1 hybrid is cross-compatible only when it serves as the female parent.

Successful intergeneric crosses have also been made between the cultivated tomato and its closely related *Solanum* species (Rick 1960; Stoeva and Zagorska 1987; Wann and Johnson 1963). A relatively loose barrier to gene exchange between species in the genus *Lycopersicon* and the feasibility of certain intergeneric hybridization with related *Solanum* species thus exist, albeit in some cases successful interchange may require the use of special techniques, e.g. embryo culture, tissue culture, bridging species (for wider crosses) , etc.

Table 3. General features of sub-genera of *Lycopersicon*

Sub-genus **Eulycopersicon**	Sub-genus **Eriopersicon**
The fruits are glabrous (hairless) at maturity and when fully developed are attractive in both taste and color, normally red or sometimes yellow; the plants are usually grown in cultivation as annuals although they can survive as perennials in frost-free conditions.	The fruits are whitish green in color, hairy and often with purplish tinge; generally not very attractive in appearance and flavor; the plants behave as perennials, dying down in adverse conditions to leave a woody stem base from which new growth emerges with the return of more favorable growing conditions.
Two species are included in the above subgenus: *L. pimpinellifolium* - currant tomato; fruits are 1 to 1.5 cm in diameter; both self- and cross-pollinated forms are known. *L. esculentum* - cultivated type; generally large-fruited but of varying sizes and shapes; self-pollinated; the wild form is *L. esculentum* var *cerasiforme* (commonly called the cherry tomato) – fruits are 1.5 to 2.5cm in diameter; the cultivated tomato is believed to have originated from this form, either directly or through hybridization with other species.	Seven species fall under the subgenus Eriopersicon: *L. cheesmanii* – self-pollinated; found only in the Galapagos Islands; fruits 6-9 mm in diameter; hybridizes easily with cultivated tomato; likely an intermediate form. *L. peruvianum* – self-incompatible; includes *L. glandulosum* ; fruits are 1 to 2 cm in diameter with lavender stripes down the midlocular axis. *L. hirsutum* – both self-fertile and self-incompatible forms known; fruits 1.5 to 2.5 cm in diameter with purplish longitudinal stripes; forma *glabratum* is self-fertile while forma *typicum* is more hairy and self-sterile. *L. chilense* – self-incompatible; fruits 1-2 cm in diameter; leaves binnatifid, covered with short hairs; inflorescence has typical long peduncle. *L. chmielewski* – cross-pollinated; fruits 1-1.4 cm in diameter; yellow-green color with relatively large calyx at maturity. *L. parviflorum* – self-pollinated; fruits are 1-1.4 cm in diameter with two dark green or purplish radial lines. *L. pennellii* – self-incompatible; formerly *Solanum pennellii*, this is another green-fruited species which hybridizes easily though unilaterally with cultivated tomato.

Genetic drift and selection for a few successful genotypes characterized the movement of tomato from its center of origin to the area of domestication and utilization(Rick 1978) . This genetic flow featured a series of changes in the floral structure–from well-exposed stigmas which facilitated cross-pollination in the primitive forms of *L. esculentum* to genetic fixation of a much shortened style in the modern cultivars (Figure 2).

The shortened style of present-day cultivated varieties places the stigma well within the anther tube, virtually eliminating the chance of outcrossing. Tomato is thus naturally highly self-pollinated. Rates of natural cross-pollination in the temperate zones vary from as low as 0.5% to as high as 4% (Rick 1978). In its native habitat in Peru, much higher rates of outcrossing have been noted because of the presence and greater activity of local insect pollinators.

The manipulation of the tomato for breeding and genetic purposes is fairly easy because its flowers are generally of good size and seed yield per fruit is high. Depending upon variety and environment, seed yield as high as 200 seeds per pollination is possible. Even without the use of mechanisms facilitating hybridity[2], e.g. male sterility and self-incompatibility, large scale production of hybrid tomato seeds is feasible because of the ease with which hybridization can be effected.

The optimum stage for emasculation of tomato flowers is a day before anthesis. Flowers at this stage have fully receptive stigma; their anthers and corolla normally show a color gradation from light to dark yellow and the sepals have begun to spread out from the bud. Dark yellow floral parts indicate fully mature flowers. Even with cautious handling, fully opened flowers should not be chosen for controlled pollination because the chance of inadvertent selfing is high.

Under isolated conditions of the greenhouse, emasculated flowers need not be bagged to prevent accidental outcrossing. The efficiency and success rate of indoor crossing are higher than in outdoor crossing. With the latter, it may also be necessary to protect flowers with glassine bags to avoid chance crosses. Cool, dry and relatively calm weather is generally favorable for field hybridization (Tigchelaar 1986).

Major Milestones in Tomato Breeding

Tomato was domesticated in Mexico and much of the credit for this very important early work must go to the native Indians who cultivated, consumed and improved the crop prior to its introduction to and adoption as a food crop in Europe and later in North America. In the latter areas, considerable progress arising from intensive research efforts happened as the crop's popularity steadily grew. In the United States, efforts by tomato scientists paid off with steady and dramatic increases in yield of processing cultivars (Figure 3). In California alone, new technology of production and improved varieties have led to four-fold increases in productivity of processing tomatoes since 1940, without which, processed tomato products would undoubtedly be a commodity that only a select few could afford (Tigchelaar 1986).

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[2] These hybridity mechanisms are present in the genus *Lycopersicon* but they have never been fully exploited in hybrid production. Self-incompatibility is a feature of several wild relatives (see Table 1) . Genetic male sterility is preponderant in the genus; many genes conditioning male sterility have been reported and described (Rick, 1956).

Table 4. Intra and interspecific breeding barriers in *Lycopersicon* [1]

⚥	*esculentum*	*pimpinellifolium*	*hirsutum*	*chilense*	*peruvianum*
esculentum	+	+	+	EA	EA
pimpinellifolium	+	+	+	EA	EA
hirsutum	+,UI	+,UI	+,SI,UI	?	EA
chilense	UI	UI	?	SI	EA
peruvianum	UI	UI	UI	EA	SI

+, no serious barrier; SI, self-incompatibility; UI, unilateral incompatibility; EA, embryo abortion; ? no known research results.

Reproductive Structures and Mating System

The tomato bears perfect flowers, i.e. it has both functional male (anthers) and female (pistil) organs (Figure 1). Several flowers are borne in an inflorescence; the number of flowers in an inflorescence may range from a few of 3 or 4 to as high as 50 in some of the cherry tomato lines (AVRDC, unpublished data). A single plant may produce as many as 20 or more successive inflorescences during its lifetime, thereby facilitating crosses among widely divergent cultivars since flowering occurs over a long period.

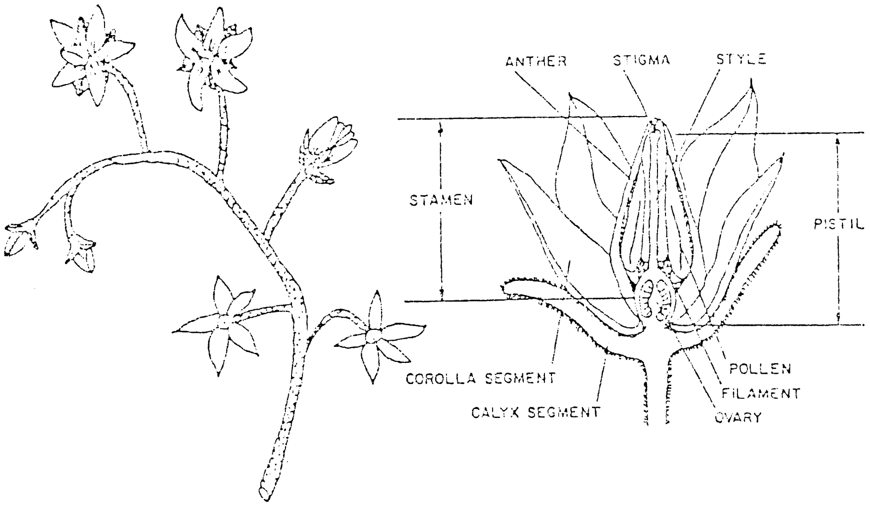

Figure 1. Diagrammatic sketch of a tomato inflorescence and flower showing all the essential parts.

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1 Adopted from Hogenboom (1972).

Evolution of self-pollination system in Lycopersicon

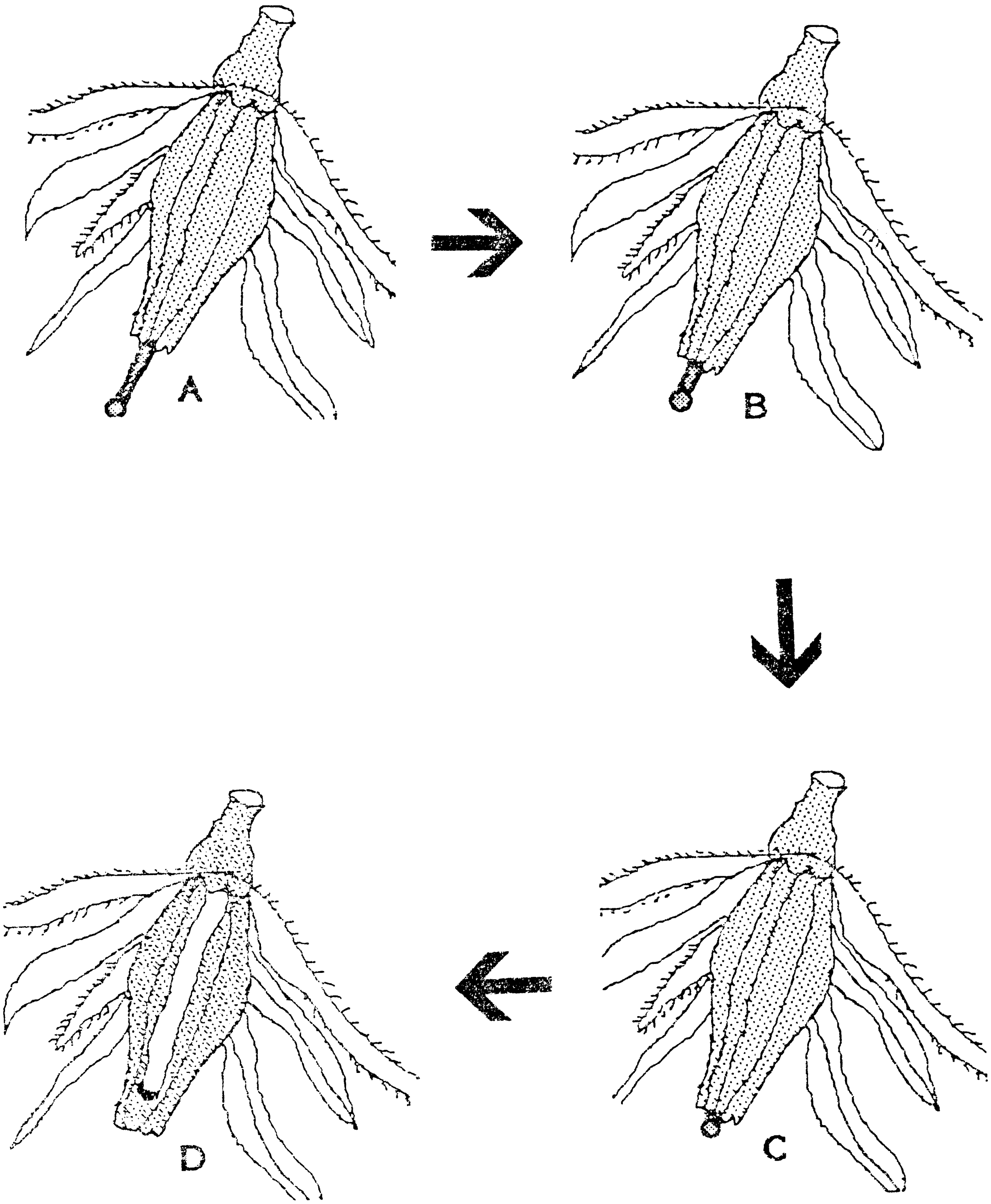

Figure 2. Progressive evolution of autogamous (self-pollination) mating system through the gradual shortening of the style, leading to well-inserted stigmas in the modern-day cultivars

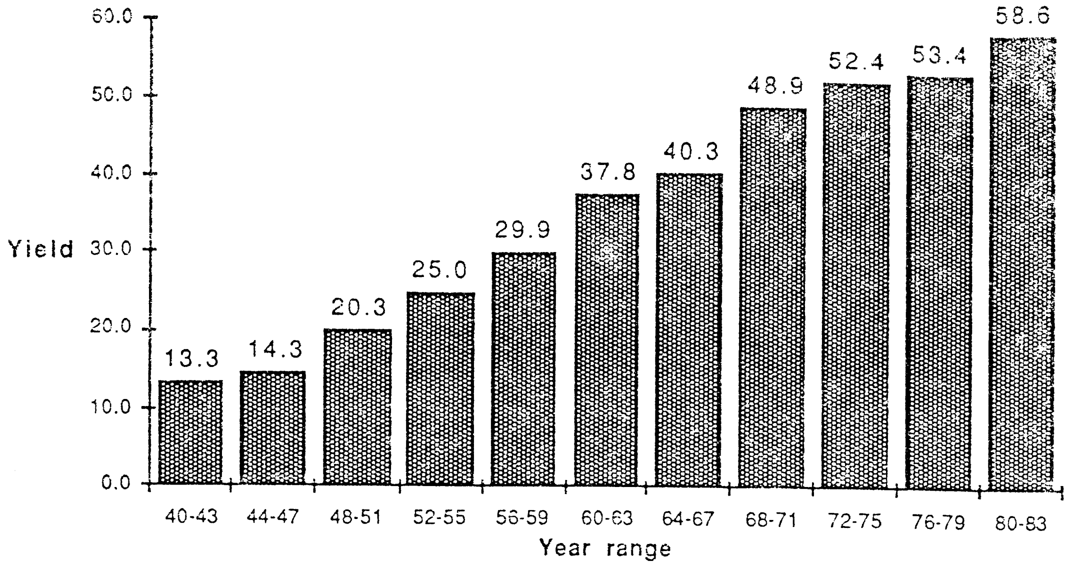

Figure 3. Progressive changes in the average yield (tons per hectare) of processing tomatoes in the United States (1940-1983)[3]

The substitution of a number of mutant genes in new cultivars has been a feature of the intense breeding activity since the 1940s (Rick 1978). One such example of a single gene with untold influence on the U.S. tomato processing industry is the self-pruning gene, *sp* , which causes the plant to grow in an orderly, compact, and determinate fashion. The *sp* gene appeared as a spontaneous mutation in Florida in 1914 and has been used in the development of a great number of cultivars in the last three decades. On account of its thrifty growth and more concentrated flowering, the determinate growth habit facilitates mechanical harvesting. Apart from changes in crop management and the design of a more suitable machine harvester, further breeding of determinate cultivars that have more compact growth, better concentration of set and with greater fruit firmness to withstand rough machine handling, along with the desirable yield, disease resistance and quality characters, paved the way for an efficient mechanization of the processing tomato production.

Other examples of major genes and polygenes that have contributed significantly in tomato improvement are given in Table 5. In particular, the genes for resistance to several major diseases have had great impact in the effective control of diseases for which chemical control has been ineffective or prohibitively costly. Good examples are resistance to soil-borne diseases such as bacterial wilt, Fusarium and Verticillium wilts.

The dominance of resistance genes for a number of diseases (among others, Verticillium and Fusarium wilts, rootknot nematode, Stemphyllium, Septoria, Alternaria, late blight, Cladosporium mold, and tomato mosaic virus) has also facilitated the development of F_1 hybrids with multiple disease resistance (Gilbert, McGuire and Tanaka 1961).

[3] Adopted and modified from Brandt (1978) and Sullivan (1977).

Table 5. Other examples of genes which have contributed to the improvement of tomato[4].

Gene designation	Gene symbol	Representative Cultivars / Lines
Dwarf	*d*	Tiny Tim
Jointless pedicel	*j-2* *j-1*	Many cultivars Penn Red
Septoria resistance	*Se*	Targinnie Red
Stemphyllium resistance	*Sm*	Chico III, Tecumseh
Leafmold resistance	*Cf* series	Many cultivars
Fusarium immunity Race 1 Race 2	 *I-1* *I-2*	 Pan American, Tainan No. 2 Walter
Bacterial wilt resistance	many recessive genes	Saturn, Venus, AVRDC tropical lines
Verticillium resistance	*Ve*	VR Moscow, VF series
Late blight resistance	*Ph-1*	New Yorker
Tomato mosaic virus resistance	*Tm-1, Tm-2, Tm-2a*	Many cultivars; AVRDC tropical lines (only *Tm-2a*)
Nematode resistance	*Mi*	Rossol, VFN Bush, many AVRDC tropical lines, many others
High pigment	*hp*	Redbush
High beta carotene	*B*	Caro-Rich
Non-ripening	nor^A	Long Keeper
Parthenocarpic fruits	*pat-2*	Severianin

In recent years, the use of F_1 hybrid cultivars has dramatically increased for fresh market tomatoes in Japan, Korea, Israel and in Eastern and Western Europe, and for processing tomatoes in California. As noted earlier, the ease of effecting crosses in tomato makes hybrid seed production feasible even with manual pollinations. As a matter of fact, virtually all hybrid seed production is manually done by highly skilled field workers. Some years ago, Taiwan was the world's leading producer of hybrid tomato seeds(Anon 1979). In recent years, however, rising cost of labor has made contractual hybrid seed production in the island comparatively expensive and contracting seed companies have begun to look elsewhere for alternative seed production sites.

While heterosis is generally minimal in self-pollinated species like tomato, the benefits of early ripening, improved vigor and the rapid development of improved cultivars which combine desirable traits such as disease resistance more than justify its exploitation in tomato improvement. Hybrid varieties also appear to have better consistency of performance especially under less than optimal growing conditions (Yordanov 1983). In addition, the added proprietary protection it gives to any new hybrid cultivar makes hybrid breeding a popular method among the private seed enterprises.

In recent years, the employment of biotechnological techniques has opened new vistas in tomato improvement that have never before been possible or would have taken long to

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4 Abridged and modified from Tigchelaar (1986).

achieve with conventional breeding. Examples of such advances are as follows: insertion of genes with insecticidal properties into the tomato genome; development of frost tolerant cultivars; and recently, development of tomatoes in which the gene that code for softening enzyme has virtually been deactivated causing the tomato to remain firm throughout full maturation. Continuing progress to 'tag' segments of the chromosome through techniques such as RFLP (restricted fragment length polymorphism) would also enable in the future an increasingly better control in manipulating complex traits and expediting the breeding process.

Commercial Types of Tomatoes as Breeding Targets

The versatility in usage and importance of tomatoes led to a great deal of specificity in developing appropriate cultivars for various purposes. Each of these purposes has, to a large extent, distinct requirements which demand fairly strict adherence before a cultivar could be successfully accepted by the growers. The distinctions between various commercial types of tomatoes are sufficiently clear that it is rare, if not outright impossible, to find a multi-purpose cultivar now. While certain objectives may still overlap, most tomato breeding programs are specially tailored to develop cultivars for specific purposes. The major types of tomatoes which serve as common breeding targets are discussed below.

Fresh market tomatoes. Tomatoes for fresh consumption have unique characteristics which depend a gerat deal upon the traditional consumer experience in the locality. In many western countries, fresh or table type tomatoes are preferably large, often more than 100 grams in weight, smooth, uniform shape, size and color, firm, good shelf-life for long distance shipping, and with good, tomato-like flavor. In some countries like Japan and Korea, pink-skinned tomatoes are preferred over the red tomatoes even though color has no known relationship to intrinsic quality.

It appears that the consumers' concept of tomato quality results partly from a general perception of the external appearance, with strong bias towards easily discernible features such as preferred skin color, rather than a definitive idea of intrinsic quality such as flavor and taste. In the United States, for example, the orange-fleshed cultivar Caro-Rich which has high vitamin A content was not accepted by the consumers even though masked color testing of the variety showed that it has comparable flavor as red-fleshed varieties (Tigchelaar and Tomes 1974; Tomes, Quackenbush and Kargl 1956). Despite the advantage in nutritional composition, it was not strong enough to override the bias towards red color. Studies in the United States indicate that flavor and taste of tomato is related to free sugars, organic acids and sugar-acid ratio (Kader *et al.* 1978; Stevens 1970; Stevens 1972; Stevens 1986; Stevens, Kader and Albright 1979; Stevens and Paulson 1976; Stevens and Rudich 1978).

In a number of tropical countries, sour, often small-fruited cultivars are preferred because they are used as ingredients in soups or local tomato-based sauces. In some cases, apparent preference for pink-colored cultivars such as in Thailand can also be noted.

Fresh market tomatoes often have indeterminate growth habit except in countries where mechanized or semi-mechanized field operations are practised. In the latter case, firm-fruited, semi-determinate cultivars such as Floradade or other later-bred cultivars are preferred as they are more amenable to mechanical operations. In some countries, determinate fresh market cultivars are grown even in the absence of an overriding need for mechanization because these are the only adapted cultivars available. Moreover, bush-type cultivars do not require costly and time-consuming staking and are thus preferred where farmers' capability to

provide inputs is limited. Where fruit quality is a premium, however, such as in large cities with substantial tourist industry to be served, indeterminate fresh market tomatoes are often demanded and cultivated.

Processing tomatoes. Tomato is processed into several major products (e.g. tomato paste, catsup, tomato juice, tomato sauce, etc) , each demanding special desirable features on cultivars that are grown for processing purposes.

In countries where the processing industry is very advanced, for example the United States or European countries like Italy, processing tomatoes are produced in extensive scale and highly mechanized, from production down to harvesting operations. Cost of manual labor in these countries are so high that mechanization appeared to be the only way they can be competitive in the international market.

To fit the cultivar to the mechanized operations, certain unique features need to be bred into them such as, among others, compact growth, firm fruits, concentrated fruit set and maturity, and ease of harvesting. These mechanization-related traits need to be combined with other desirable horticultural traits such as disease resistance, good canopy to minimize sun scorching, some level of stress tolerance to minimize split set and insure an undisrupted harvesting schedule, improved yield at no sacrifice in quality, earliness, etc.

Quality of processing tomatoes are normally measured in terms of color, soluble solids, pH, total acidity, total solids and viscosity. Some of these parameters are especially important for certain processed products. For example, viscosity (or consistency) is a primary quality attribute influencing catsup production. On the other hand, the tomato paste processing standard depends upon the final soluble solids content of the finished product, thereby demanding the use of high soluble-solids cultivars or adoption of management practices that maximize soluble solids of harvested tomatoes.

For less advanced processing tomato production, such as those in tropical and subtropical countries, the above-mentioned quality features are more often wished for but not necessarily obtained. Processing tomatoes under these conditions often have inferior color and relatively low solids content. Even with the use of cultivars of relatively high solids content, the growing conditions are not generally favorable for processing tomato production and management practices are not fine-tuned enough to achieve relatively high soluble solids content in the harvested tomatoes. Apart from processing quality, processed products are often insufficient for domestic consumption.,

Other special types. Tomato cultivars have also been developed for other special purposes, a glowing evidence of the popularity and the diverse business and personal interests of tomato growers and gardeners. For example, there are cultivars that are specifically bred for greenhouse production. These cultivars are generally indeterminate in habit and are productive for several months, medium to large-fruited, relatively uniform in size within the individual clusters, and carry resistance to diseases that are much more common in the greenhouse culture than in the outdoor production, such as tomato mosaic virus, leaf mold (*Fulvia fulvum*) , and gray mold (*Botrytis cinerea* Pers.).

Other diverse types that have been bred belong mainly to home-grown tomatoes and are developed to suit the fancy of consumers who prefer to savor the fruits of their toils by growing their own tomatoes in their backyard (home-garden type) or in small pots (patio-type tomatoes). Desirable features of these tomatoes include earliness, disease resistance, good quality, and prolonged production. In some cases, novelties such as unusual color (orange or yellow), dwarf habit for potted patio culture, unique fruit shape, etc. contribute to popularity of home-grown cultivars.

While cherry tomatoes are not new, recently bred cultivars have stimulated the interest of tomato growers in Japan, Korea, Taiwan and the United States. In Taiwan, cherry-type varieties, such as Girl Sweet and Len-tzu, are now grown by farmers for a special fresh use[5].

Common Breeding Objectives

High yield. Nearly every breeding program has high productivity as one of its major goals. Yield *per se* is the end product of a chain of interacting processes, each under a genetic system of control that may themselves be unique but often interrelated with the genetic systems underlying other processes. Genetically thus, yield is complex and invariably influenced by environmental factors.

The genetic control of yield is invariably polygenic (i.e. the trait is controlled by many genes with small effects and are highly influenced by environmental factors) ; also, additive and non-additively acting genes are known to condition yield. As a result, selection for high yield demands a rigorous control of environmental effects to insure that the phenotypic expressions of the breeding materials closely correspond to their true genetic potential.

Depending upon the predominant gene action, breeding techniques may be accordingly modified to attain maximum breeding gains. For example, where non-additive gene action is significant, hybrid breeding may be worthwhile to undertake especially if there are other overriding advantages of hybrid varieties in a given circumstance. On the other hand, conventional selection and development of standard open-pollinated cultivars prevail when additive gene action predominates, especially where seed companies do not play a major role in the vegetable seed industry.

Yield per unit area of tomato is a product of several components–plant stand, number of functional clusters, number of fruits per cluster, and fruit weight. Increasing yield may appear as simply maximizing each component. However, while each of these components may be linearly related to yield, they do interact with each other, often in compensating ways, resulting into a more complex rather than the simple arithmetic relationship between yield and its components. For example, increased fruit number per cluster or total fruits per plant means reduced mean fruit weight.

While yield components of tomato intimately determine gross yield, the final marketable yield is influenced by a number of other factors, mostly related to quality reduction. Defects such as sunscald, cracking, soft and diseased fruits, abnormal shapes, unattractive features such as fasciation and catfacing, poor color, and blotchy ripening contribute to the diminution of final yield. Therefore, breeding programs may effectively attain (or perhaps more appropriately, insure) high yield through obvious means such as breeding for resistance or tolerance to factors promoting these defects. Breeding for disease resistance also achieve the same effect–reducing disease-caused blemishes or rotting of fruits and maintaining the desired field stand.

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[5] Cherry tomatoes are partly sliced and either date or bean sauce is placed inside to add to the flavor. Fruits, in general, are sweet and crispy (on account of thick and tough skin).

Tolerance to biotic stresses. Biotic stresses refer to all disease and pest factors affecting the productivity of tomatoes. No doubt, biotic stresses are among the major yield and quality-limiting constraints, if not the most important, in tomato production. In view of this, tomato breeding programs always include breeding for pest resistance, especially disease resistance, as one of the major objectives.

The development of disease-resistant tomato cultivars is perhaps one of the most important contribution of modern plant breeding to tomato improvement (Tigchelaar 1986). There are a number of economically important diseases for which control is either absent or prohibitively costly (e.g. soil-borne wilt diseases such as bacterial wilt, fusarium wilt, etc). Exploitation of host plant resistance in breeding gave rise to resistant cultivars which made production in infected fields economically feasible. With the vital collaboration of plant pathologists, tomato breeders have successfully bred increasingly more disease-resistant breeding lines.

Progress in developing disease-resistant tomatoes would not have been possible without the genetic resources to sustain the breeding efforts. Fortunately, the genus *Lycopersicon* is a treasure trove of genetic variability (see Section Genetic Diversity). Genes for resistance to various diseases have been uncovered from cultivated and wild relatives of tomato and in many cases, their underlying inheritance are also well known (Table 6; see also Table 5 for examples of genes controlling resistance to several diseases and resistant cultivars).

While much of the advances in tomato research, particularly disease resistance, has been achieved in the temperate countries, the tomato research at AVRDC in Taiwan has undoubtedly contributed to enable profitable tomato production in the tropics. A great part of this feat owes much on the early development of breeding lines that are resistant to bacterial wilt, followed by a progressive pyramiding of additional genes for resistance to other major tropical diseases, particularly tomato mosaic virus and common rootknot nematode (Opeña, Kuo and Yoon 1987a; Opeña *et al.* 1988; Opeña *et al.* 1987b). The incorporation of additional resistance to diseases such as bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*), black leafmold (*Cercospora fuligena*) and potato virus Y is underway and stands to further improve the reliability of tomato production under adverse tropical growing conditions.

Insect resistance breeding in tomato has not been as successful as disease resistance breeding. The difficulty does not appear to be due to restricted variability for insect resistance; as a matter of fact, the genus *Lycopersicon* is replete with good reports on resistance to various mites and insect pests (Table 7). Several reasons attribute for the lack of progress in insect resistance breeding: first of all, insect resistance has traditionally received low priority in applied breeding programs because the use of pesticides has effectively controlled most of the major insect pests of tomato; in addition, the screening and selection methods to exploit the existing genetic variability for insect resistance are difficult to develop.

With the exception of a few cases, the genetic resources for insect resistance in tomato exist mainly among the wild species (see Table 7). Of these wild relatives, the most prodigious reservoir are the species *hirsutum* and *pennellii*. Efforts to utilize these species to breed insect-resistant tomato breeding lines are now underway at AVRDC for pests such as fruitworm (*Heliothis zea*) and aphid (*Myzus persicae*) . The potential impact of insect-resistant

Table 6. Sources of resistance and inoculation techniques for screening tomato diseases[6]

Disease	Causal organism	Source of resistance	Inoculation techniques
Fusarium wilt	*Frsarium oxysporum f. sp. lycopersici* (Sacc.)	Pan American (race 1), Walter (race 2)	Dip roots in inoculum and transplant to flats
Verticillium wilt	*Verticillium albo-atrum* Reinke & Berth	VR Moscow	Dip roots in inoculum and transplant to flats
Late blight	*Phytophthora infestans* (Mont.) DBy	West Virginia 63	Inoculate leaves with swarmspore suspension by atomization
Early blight	*Alternaria solani* (Ell. & G. Martin) Sor.	(on foliage) 68B134	Inoculate with atomized spore suspension
		(collar rot) Southland	Dunk tops and stems of seedlings into inoculum and transplant to a depth of 3 in
Septoria leaf spot	*Septoria lycopersici* Speg.	Targinnie Red	Atomize conidial suspension onto plants
Gray leaf spot	*Stemphylium solani* Weber	Manalucie	Atomize spore suspension onto plants
Leaf mold	*Fulvia fulvum* Cke.	Sterling Castle	Inoculate by spraying lower-leaf surfaces with spore suspension
Foot and stem rot	*Didymella lycopersici* Kleb.	*L. hirsutum* 66087 (IVT 61292)	Apply 3 ml of inoculum around the stem base of 1-week-old seedlings
Brown root rot (corky root)	*Pyrenochaeta lycopersici*	PI 260397	Plant to fields infested with the causal organism
Anthracnose	[*Colletotrichum phomoides* (Sacc.) Chester] C. *coccodes* (Wallr.) Hughes	PI 272636	Inoculate fruit by atomization or puncture
Rhizoctonia soil rot	*Rhizoctonia solani*	PI 193407	Place mature green fruit on infested soil

(Continued)

6 Adopted from Webb *et al.* 1973.

Disease	Causal organism	Source of resistance	Inoculation techniques
Bacterial wilt	*Pseudomonas solanacearum* (E.F. Sm.) E.F. Sm.	PI 127805A Saturn Venus	Cut roots on one side; pour bacterial suspension into soil trench
Bacterial canker	*Corynebacterium michiganense* (E.F.Sm.) H.L.Jens.	Bulgarian 12, Utah 737	Inoculate cut made by excising first true leaf at point of attachment with bacterial suspension
Bacterial speck	*Pseudomonas tomato*	Ontario 7710	Atomize suspension of *P. tomato* on both sides of leaf
Tomato mosaic	Tobacco mosaic virus	Ohio M-R9	Apply expressed inoculum with an air brush; inoculate again 10 days later
Spotted wilt	Spotted wilt virus	Pearl Harbor	Place seedlings in a disease nursery and encourage thrips
Curly top	Curly top virus	CVF 4	Release viruliferous leafhoppers into screened green house 2 or 3 times at 1-week intervals
Yellow leaf curl	Yellow leaf curl virus	*L. pimpinellifolium* (LÁ 121)	Release viruliferous whitefly females onto caged tomato seedlings; allow feeding for 72 hr.

cultivars in the tropics is tremendous, considering the relative difficulty and prohibitive costs of controlling pests by inorganic chemicals. Eliminating the use of pesticides that are generally hazardous to health and threatening to the integrity of our environment is probably the most noble justification to intensify the efforts in insect-resistance breeding.

Apart from diseases and insects, tomato is also attacked by nematodes, causing devastating losses where they are endemic. Among 37 recognized rootknot nematode species (*Meloidogyne* spp), seven are known to attack tomato of which *Meloidogyne incognita* is the most prevalent and of major importance in tomato production (Taylor and Sasser 1978). Losses due to direct infection (Bailey 1941; Baker, Shoemaker and Nelson 1976; MacFarlane, Hartzler and Frazier 1946) and indirect losses due to predisposition or breakdown of resistance to other root diseases, e.g., bacterial wilt (Gilbert, Tanaka and Takeda 1974) are significant. Much like many other diseases, breeding for resistance offers the most economical long-term solution.

Table 7. Genetic resources for resistance to various mites and insect pests of tomato.[7]

Insect pest	Source of resistance	Species
Flea beetle (*Epitrix hirtipennis*)	PI 126449	*L. hirsutum* f. *glabratum*
Potato aphid (*Macrosiphum euphorbiae*)	PI 129145	*L. peruvianum*
Spider mite (*Tetranychus telarius* L.)	Anahu	*L. esculentum*
Carmine spider mite (*Tetranychus cinnabarinus*)	Several accessions	*L. hirsutum*
Colorado potato beetle (*Leptinotarsa decimlineata*)	PI 134417	*L. hirsutum*
Pinworm (*Keiferia lycopersicella*)	PI 127826	*L. hirsutum*
Leaf miner (*Liriomyza munda*)	PI 126445, PI 126449	*L. hirsutum* f. *glabratum*
Fruitworm (*Heliothis zea*)	PI 126449	*L. hirsutum* f. *glabratum*
Tobacco hornworm (*Manduca sexta* L.)	PI 134417	*L. hirsutum* f. *glabratum*
Whitefly (*Trialeurodes vaporariorum*)	IVT 74453 IVT 72100	*L. hirsutum* *L. pennellii*

Bailey (1941) reported *L. peruvianum* as a source of resistance to rootknot nematode. The first interspecific hybrid between *L. peruvianum* and cultivated tomato was made in 1944 using the former as male parent to overcome the unilateral incompatibility barrier and rescuing the immature embryo through aseptic culture to surmount hybrid breakdown (Smith 1944). Further backcrosses using cultivated tomato as the male parent led to the independent development of cultivars VFN-8 and Anahu in California and Hawaii, respectively. This resistance is controlled by a single dominant gene *Mi* (Barham and Winstead 1957; Gilbert and McGuire 1956) and provides resistance to three other prevalent nematode species (*M. javanica, M. arenaria*, and *M. acrita*).

A tight linkage between the *Mi* gene and *Aps-1*, a variant locus of acid phosphatase isozyme was discovered on cv. VFN and other nematode-resistant cultivars (Rick and Fobes 1974). This discovery led to the practical use of electrophoresis in screening for nematode resistance in the laboratory to complement or replace other methods of resistance screening that had been proposed in the past (Bailey 1941; Dropkin, Davis and Webb 1967; Fassuliotis and E. C. Corley 1967). A number of resistant cultivars from many sources were studied (Medina-Filho and Stevens 1980) ; cultivars with pedigrees tracing back to Hawaiian materials did not show the *Aps-1* band pattern. On the other hand, those derived from California resistant stocks maintained the linkage relation between *Aps-1* and *Mi* genes. A linkage test between these genes was carried out and it was concluded that nematode resistance screening

[7] Modified after Tigchelaar, 1986.

based on the *Aps-1* banding pattern was remarkably reliable (Medina-Filho and Stevens 1980).

Tolerance to abiotic stresses. Tomatoes thrive and produce well under generally cool and dry climate. Any significant deviations from this ideal condition, sush as high temperatures and excessive rainfall, generally result into depressed tomato yield and quality. Fruit set is one of the key components of final yield in tomato (Picken 1984; Stevens and Rudich 1978) that is greatly affected by adverse conditions, particularly high temperature (Opeña *et al.* 1987a). Both night and day temperatures are considered important to tomato fruit set (Sugiyama, Iwahori and Takahasi 1966). Maximum temperatures below 30°C favored fruit setting and yield; ranges between 30°-45°C markedly reduced fruit set (Went 1945). Poor fruit set at high temperature might result from the reduction of carbon export from the leaf and the inability of reproductive organs to import assimilates in the early stages of flower development (Dinar and Rudich 1985; Dinar, Rudich and Zamski 1982).

Heavy rainfall may mechanically damage the aerial parts of plants, but topogenic water accumulation due to poor surface drainage may also lead to damaging flooded conditions. One principal effect of flooding is the rapid depletion of soil oxygen supply from the roots. The effect of oxygen deficiency on plants is complex, comprising of direct, physiological effects of low oxygen supply, and the indirect, oxygen-dependent changes in the soil; these factors are difficult to separate. Visual symptoms due to deficient aeration may appear on the roots and shoots. The characteristic symptoms of flooding damage in the tomato shoots are: a) reduced stem growth; b) chlorosis of the lower leaves; c) marked epinastic curvature or wilting of the leaves; d) production of adventitious roots; and e) death of the plants.

The primary cause of the above growth disturbances is the inhibition of aerobic respiration in the roots (Drew 1979). Other adverse effects on the plant's vital functions such as growth, water uptake, and nutrient uptake, are the consequences of abnormal respiration. The exclusion of oxygen from root metabolism also causes ethanol accumulation and ethylene elevation (Bradford and Yang 1981). Toxic effects of ethanol on plant tissues and the association of ethylene, epinasty, and adventitious root formation are known (Kuo and Chen 1980; Kuo *et al.* 1982).

Breeding for stress tolerance in tomatoes, particularly to high temperatures, has been carried out at AVRDC since 1972. Heat tolerance in tomato was defined as the ability to set fruits under night temperatures not lower than 21°C (Villareal and Lai 1978). This trait reportedly gave strong indications of genetical complexity–variation was continuous and heritability values were low, with a range of only 5–19% (Villareal and Lai 1978).

Defined on the basis of fruit set, heat tolerance implies an ultimate product of a complex reproductive process; therefore, attempts have been made in the past to examine the components, rather than the end product of the trait, so as to deduce relatively simple genetic situations. For example, stigma exsertion, one of the common responses of heat-sensitive cultivars under high temperatures, was found to be controlled by partially dominant genes with high additive component and heritability (El Ahmadi and Stevens 1979; Levy, Rabinowitch and Kedar 1978; Stevens 1979). These results corroborated well with the outcome of an earlier study (Rick and Dempsey 1969).

Further studies of a genetically diverse seven-parent diallel set showed that both additive and non-additive genes are important in regulating the fruit set at high temperature (AVRDC 1988). A similar genetic behavior was noted for the splitting of the antheridial cone, a common reaction of tomato flowers to high temperature.

Based from the above study, it was concluded that both conventional breeding methods, which take advantage of additively acting genes, and hybrid breeding, which relies primarily on genetic interactions, should be effective in breeding for heat tolerance. In support of the latter, about 1/3 of the diallel hybrid progenies from the foregoing study had better fruit set than the better heat tolerant parents (AVRDC 1988).

In a related study, crosses between heat tolerant stocks were noted to have better fruit setting ability and yield than their crosses with heat sensitive parents (Figure 4). However, it was apparent from the range of F_1 means (Table 8) that some hybrids between heat tolerant and heat sensitive stocks could equal, if not surpass, the performance of hybrids among heat tolerant stocks, further supporting the results from the diallel experiment (Opeña *et al.* 1987a).

Improved Quality. Aiming for improved quality through breeding is freqrently only a wishful thinking because the parameters that affect quality are generally nebulous. Moreover, the criteria of good quality vary among consumer groups. The subjectiveness of quality introduces a great deal of complications in its genetic improvement. Quality is, therefore, often only a secondary priority in the breeding program. Nonetheless, every breeder must insure that the resulting product of breeding must, at the very least, conform to the acceptable norms of quality. Often, this involves merely insuring that the new culitvars are not exceedingly off-flavored or of poor external appearance.

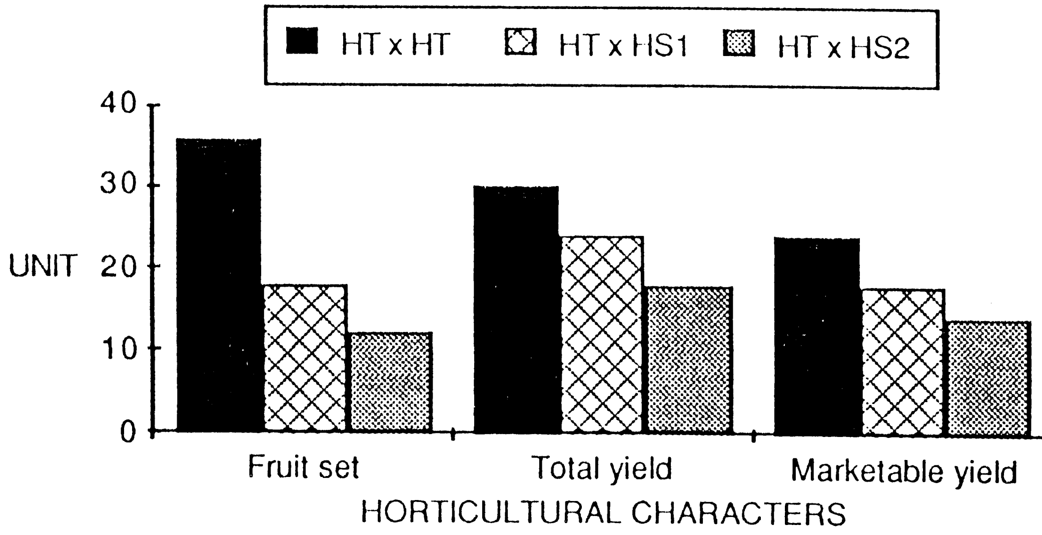

Figure 4. Comparative fruit set (%) and yield (t/ha) of F_1 hybrid progenies derived from crosses among parents with varying levels of heat tolerance (abbreviations in the legend footnoted in Table 8).

Table 8. Range of values for different characters among tomato hybrids with differing levels of heat tolerance (exceptional upper range values are underscored).

Type of cross[z]	No. of crosses	Fruit set (%)	Yield (tons / hectare) total	Yield (tons / hectare) marketable	Fruit size (g)
HT / HT	8	26-52	15.4-37.5	12.3-29.0	41-63
HT / HS1	11	5-30	15.9-28.8	9.8-23.2	57-83
HT / HS2	10	2-32	6.3-33.2	5.9-27.6	59-92

[z] HT = heat tolerant parent; HS1 = heat sensitive parent (less than 10% fruit set) ; HS2 = heat sensitive parent (no fruit set).

While the above may be a common scenario in tomato breeding, there are aspects of tomato quality that could be reasonably improved in a breeding program. The tomato fruit is about 95 to 96% water. The remaining 4 to 5% are comprised of organic constituents such as organic acids, free sugars and volatiles. This fraction generally gives the tomato fruits its unique flavor, taste, aroma and texture (Stevens 1979; Stevens *et al.* 1979; Stevens and Rudich 1978). Dramatic changes occur on these constituents as the tomato fruits mature. There are indications that some, if not all, of these constituents are fairly simple in inheritance and are, therefore, amenable to genetic improvement (Stevens 1970; Stevens 1972; Stevens 1976; Stevens 1986).

Breeding for improved appearance often receives higher priority over the intrinsic aspects of quality. This is understandable when one considers that consumers often have bias towards what they can see and perceive. Size, shape, external color, smoothness of the fruit surface, firmness, uniformity and freedom from defects such as cracking, catface and fasciation are generally important breeding objectives especially for table tomatoes. Some of the above may also be important for processing tomatoes (such as fruit color, firmness and crack resistance) but generally less so than with fresh market types since tomato fruits for processing are crushed and concentrated into various processed forms.

Considerable progress has been obtained in developing cultivars that are both firm and resistant to cracking (Reynard 1960; Scott 1983). With respect to fruit color, many genes affect the trait (Darby 1978) , of which, for practical purposes, genes *hp* and og^c have been explored to enhance the redness of tomato fruits (Thompson 1961). With good practise, both *hp* and og^c may be visually assessed among breeding progenies. Gene og^c increases the red pigment "lycopene" but does so at the sacrifice of reduced β-carotene and thus, lower vitamin A content of the fruits. In contrast, gene *hp* increases total carotenoids thereby rendering excellent color to the fruit and enhanced vitamin A content. However, several undesirable pleoitropic effects of *hp*, such as slow germination, thrifty growth, and premature defoliation, have discouraged its use in tomato improvement programs (Kerr 1965; Sayama and Tigchelaar 1985; Wann *et al.* 1985).

Breeding Techniques

The most fashionable breeding technique to improve tomato has been hybridization followed by pedigree selection. Single-seed descent method was developed later and has been used as an alternative to pedigree selection where facilities or funds do not permit copious and time-consuming record-keeping from breeding materials, or to develop a diverse range of "ready-to-test" breeding lines for trial and selection by national programs which lack breeding expertise to undertake full-scale breeding programs (Villareal and Lai 1979) , or where facilities to maintain winter breeding nurseries are limited (Tigchelaar 1986). Backcross breeding has been the method of choice when desirable traits are to be transferred from the wild species or from relatively unimproved cultivated varieties. In some breeding programs, combinations of methods such as pedigree breeding and single-descent have been found to be a useful approach (Casali and Tigchelaar 1975). A number of breeding techniques are further discussed below.

In most cases, the breeder's goal is to develop improved standard, open-pollinated cultivars. However, in the last decade or so, the use of hybrid cultivars has increased dramatically that in several countries, they have almost replaced the standard cultivars in fresh market tomato production (see Section Major Milestones in Tomato Breeding). The major role played by the private seed sector in developing and distributing improved tomato cultivars has encouraged the trend towards increasing use of hybrids. Irrespective of the final type of cultivar to be developed, the breeding techniques that are used to develop the improved standard cultivars and/or inbred parents for hybrid varieties are one and the same. In developing hybrid varieties, however, this is further extended to select from among the inbred stocks those that nick well to produce superior hybrid progenies. This normally entails the application of progeny testing methods such as combining ability test, especially where a great number of parental stocks are being exploited. In certain situations, conscious breeding for traits which facilitate emasculation of tomato flowers, such as genic male sterility, may also be done as an accessory of hybrid breeding.

Selection methods for naturally occuring variation. Old land varieties or, even local cultivars that have been grown for sometime under a certain environment without conscious selection by farmers themselves, are considered as populations of pure lines[8]. Before any long range breeding program of hybridization and selection is conceived, plant breeders must first explore the genetic materials on hand. Old local cultivars which have well-proven adaptability under certain conditions are often available. Sometimes, introduced cultivars which do well under a particular condition may exhibit some degree of utilizable variation. Breeders need to examine these materials closely to see if simple selection procedures can bring in further improvement. When substantial variation is available, mass selection will allow the elimination of undesirable individuals and, at the same time, preserve the characteristics that have made these cultivars successful. Afterwards, pure line selection could be applied to further identify the most superior, homozygous lines for eventual release to the growers.

Mass selection. This may be achieved by simply growing the variety in the field and roguing out the undesirable types. At maturity, the remaining plants (presumably the good plants) are bulked. A modification is tagging only the best plants in the field and bulk-

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[8] Technically, a pure line is the collective term for progenies of a single, self-fertilized homozygous individual.

harvesting them at maturity. The two methods are essentially similar, the only difference being in the level of selection intensity. Modern plant breeding usually employs mass selection to preserve the characteristics of established varieties.

Pure-line selection. This is a refinement of mass selection. The method involves also tagging (selecting) the best plants of the variety. However, instead of bulk-harvesting these plants as in mass selection method, they are harvested separately and evaluated as distinct progeny rows (pure lines). Only the superior pure line is bulked as an improvement of the variety. The pure line may even be released as a new variety if it is sufficiently different from the original variety.

Selection methods for variation generated through controlled hybridization. Following hybridization, a tremendous burst of variation is released after selfing the immediate hybrid progeny of the cross. Successive self-fertilizations of the hybrid progenies of self-pollinated crops lead to the progressive decay of the variability within individuals, but with concomitant accentuation of the variation among individuals. The variability can be managed by different methods, ranging from simple systems (such as single-seed descent and bulk method) to more tedious and elaborate techniques (such as the pedigree method). Each technique has its own merits and demerits and their application depends upon a number of factors such as manpower, land and financial resources, level of expertise, timetable, objectives, crop species, etc.

Pedigree method. As the name denotes, pedigree method involves taking a record of the line of descent (or "pedigree") of individuals or lines selected in each generation. These notes are very important in deciding which lines to keep or eliminate. The information to accumulate may range from notes of general vigor, maturity, resistance to some diseases or pests, quality, etc.

The pedigree method offers the plant breeder an opportunity to sample families of diverse descent. For example, if two lines behave similarly, one could be eliminated if they are closely related according to the pedigree record. This aid in decision-making offered by the pedigree record clears the way for the breeder to select another unrelated line out of the same cross.

In using pedigree selection, the breeder must keep in mind the changing architecture of variability. The greatest range of variability will be expressed in the F_2 generation; thereafter, the level of heterozygosity in the population will decrease rapidly upon selfing with a concomitant increase in proportion of homozygosity (and homozygous genotypes). Based on this trend, selections in the first few generations (F_2, F_3 or even F_4) will be concerned mainly with single-plant performance. Selections in later generations (F_5 and on) must shift towards line or family performance as the within-line variability becomes increasingly dissipated.

The pedigree selection method may be illustrated as in Figure 5 below.

Other notes of importance to pedigree selection are as follows:

(1) F_2 population provides the first opportunity to practise selection. Thus, progenies should be space-planted to facilitate the identification of superior types. Check varieties (one or the other parents or a successful cultivar) are planted every few rows, e.g. every 10th row, for comparison with the progenies. Oftentimes, undesirable progenies are eliminated as soon as they become visible. From the remaining plants, the best plants that exhibit the characteristics desired in a new variety are selected.

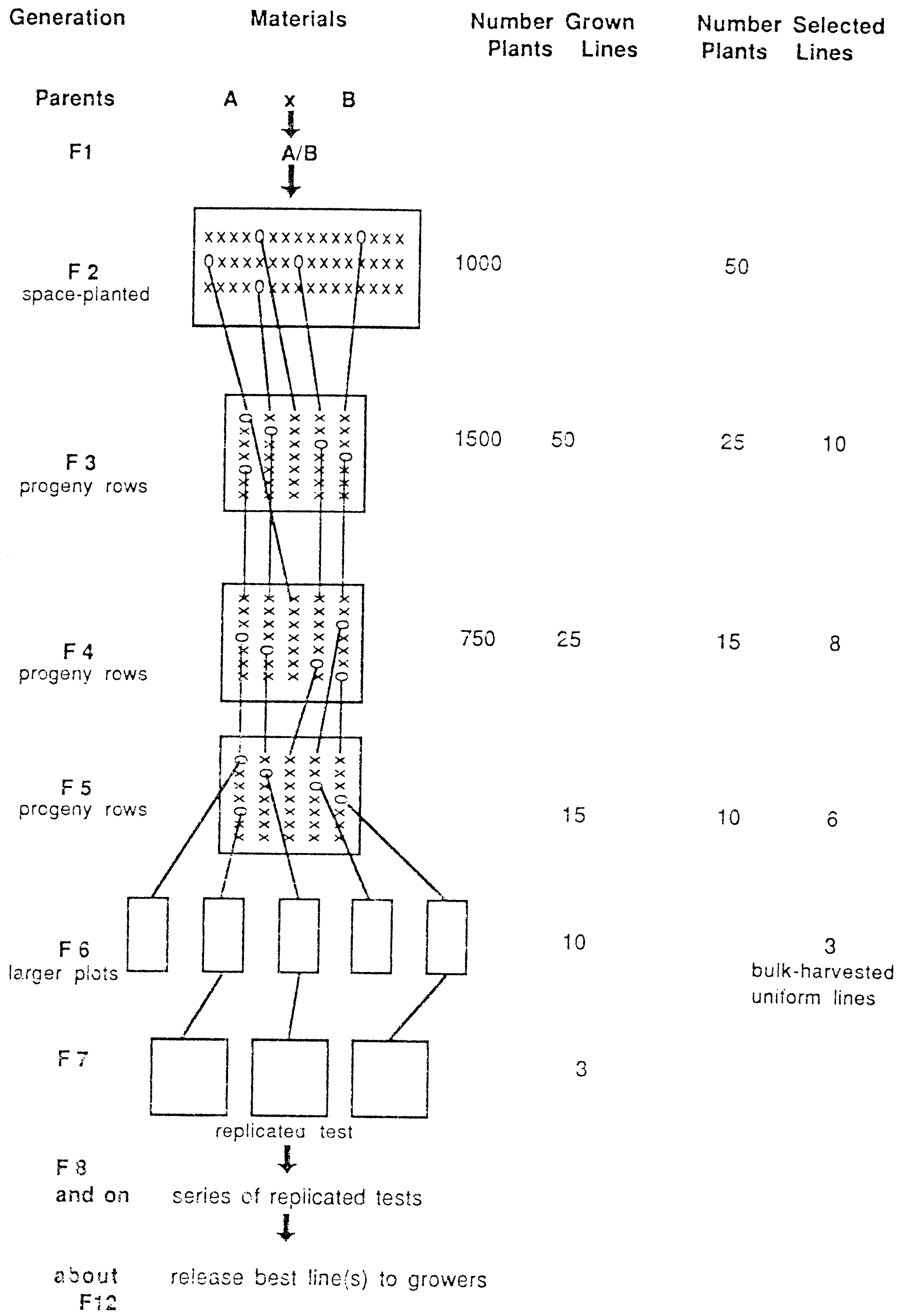

Figure 5. Diagrammatic sketch of pedigree selection method as applied to self-pollinated crops.

(2) F_3 families are also space-planted but normally at intervals closer than F_2 plants. Thirty-forty plants are usually grown to each F_3 family and check rows are again included. The potential of the cross will become apparent in the F_3. Single plant selection is again practised, selecting mainly from superior families but not neglecting superior progenies in otherwise poor families.

(3) Handling the F_4 generation is more or less similar to F_3. Sometimes, breeders prefer a shorter, multiple rows rather than a single long row for better visualization of the line potential. Many F_4 families will appear quite homogeneous but not in any magnitude that will suggest bulk-harvesting them. Still, single-plant selection are practicable, selecting only from mostly superior families. A combination of pedigree record and visual evaluation should lead to a substantial reduction in population size.

(4) Larger plots are used in the F_5 and spacing may approximate the commercial conditions. Single-plant selections are made usually from uniform families (they are therefore assumed to be largely homozygous). The bases of selection are pedigree record and visual appearance and possibly yield, if plots are large enough.

(5) The F_6 generation and beyond are considered non-segregating. Selection is shifted from single plant to family performance. Planting rates approximate as closely as possible the commercial conditions. Selected uniform families are harvested in bulk within each to provide sufficient seed stocks for the subsequent replicated trials.

Some modifications of the pedigree method that had been suggested involved: crossing superior selections in early generations or crossing of selections at random in the early generations. Both procedures are designed to slow down the approach to complete homozygosity and thus, enhance the chances of obtaining superior genetic combinations. The applicability of these modifications will depend on crop species–when crosses can be made easily, it should be appropriate to adopt them especially where linkage of traits under consideration are involved. They would be impractical, however, if crosses are difficult to make.

Pedigree method offers the following advantages: it permits elimination of a great number of unpromising materials in early generations; it allows evaluation of selections on the basis of several year's performance; and, it enables sampling more diverse materials from each cross.

However, the method is time-consuming, very tedious and therefore, severely limits the number of crosses that can be exploited as sources of superior genotypes.

Bulk method. Another simple and less time-consuming method of handling segregating progenies from hybridization involves growing them *en masse* from F_2 and succeeding generations until the desired homozygosity is achieved. The method allows natural selection, with the aid of the breeder, to gradually weed out the undesirable types within the population so that after a few generations only the most adapted forms are expected to remain. At this point, when such forms are already genetically stable (homozygous) , single plant selections are made and evaluated in a series of trials. Only the best line (s) are released.

Since very little work is required, bulk method allows several crosses to be handled at one time and large populations of each cross can be grown in each generation, thereby increasing the possibility of greater gene combinations. The bulk method is illustrated in

Figure 6 below. Sometimes, bulk method is modified in a manner that only the best plants in each generation (from F_2-F_5) are bulked. This is called modified bulk method.

Single-seed descent (SSD). As the name implies, breeding progenies in each generation are descended, technically speaking, each from a single seed. Usually, there is no selection from generation F_2 up to F_6 or F_7; as many plants as possible from the F_2 are carried down to F_6 or F_7 (at this time, the population will be made up largely of homozygous individuals). Evaluation of F_6 or F_7 lines and generations thereafter is carried out to select the superior combinations out of the cross.

SSD is very simple and could be a rapid method if manipulations of plant growth and development are done. Oftentimes, progenies are grown in the greenhouse to minimize losses in population size. This procedure will, however, require large greenhouse space and therefore, will allow handling of only a limited number of crosses. The underlying principle is to bring a wide range of the variability originally present in generation F_2 to a testable stage such as F_6 or F_7 where most lines would be genetically stable already.

A modification of SSD method often includes selection in the intervening generations especially for highly heritable traits (characters that are expressed strongly in single plants and not easily influenced by environment, e.g. disease resistances controlled by major genes). A good selection regime (or screening technique in the case of disease resistance) must be available however.

Assuming that two varieties are crossed to combine their desirable characteristics, a typical SSD method would be carried out as in Figure 7 below.

Backcross method. Literally speaking, backcross means "crossing back". The procedure is carried out using one of the original parents as a constant parent and the immediate or selected progenies from a segregating backcross generation as the other parent, depending upon the behaviour of the gene (s) under consideration. The constant parent is technically termed "recurrent parent". The other original parent which contributed the gene (s) under transfer to the recurrent parent is called "donor parent".

The objective of the backcross method is to transfer a gene or genes from the donor to the recurrent parent, recovering as much of the genetic background of the latter as desired. This implies that the recurrent parent must already be a successful variety, lacking only the gene (s) available from the donor to be truly outstanding. It also implies that the donor parent carries the gene (s) to be contributed in the most intense form.

The backcross method is especially applicable when the donor parent is a commercially unadapted type (e.g. wild species) so that straight hybridization and selection will not reasonably lead to superior genetic combinations. Often, the unadapted parent carries, along with the desired gene, a number of undesirable genes. Assuming no unfavorable linkage, backcross method will allow the transfer only of the desirable gene (s) , eliminating the undesirable traits in the backcrossing process. The method has been very useful in disease resistance breeding, where often only a few genes are being dealt with and therefore, the breeder is able to establish a firm control over the genetic circumstances.

For simplicity, assume that a single dominant gene for disease resistance is being transferred from a donor variety and that this gene is inherited in a dominant fashion. Using the letter "R" as gene symbol, *RR* and *Rr* would be resistant and *rr* is susceptible. In this situation, the donor parent is *RR* (resistant) and the recipient or recurrent parent is *rr* (susceptible). Under this given condition, the backcross method would be carried out as illustrated in Figure 8 below.

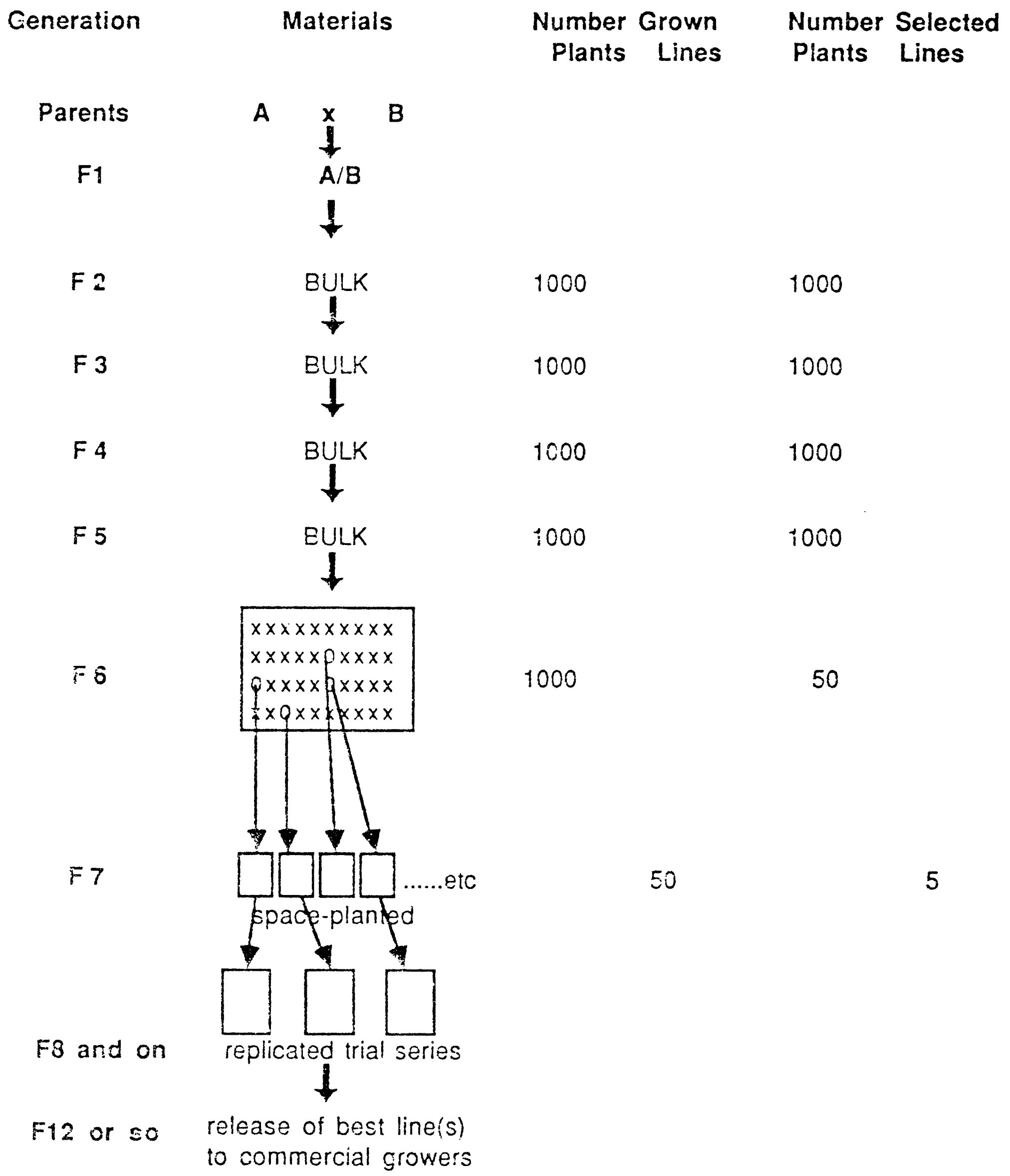

Figure 6. Diagrammatic sketch of the bulk method as applied to self-pollinated crops.

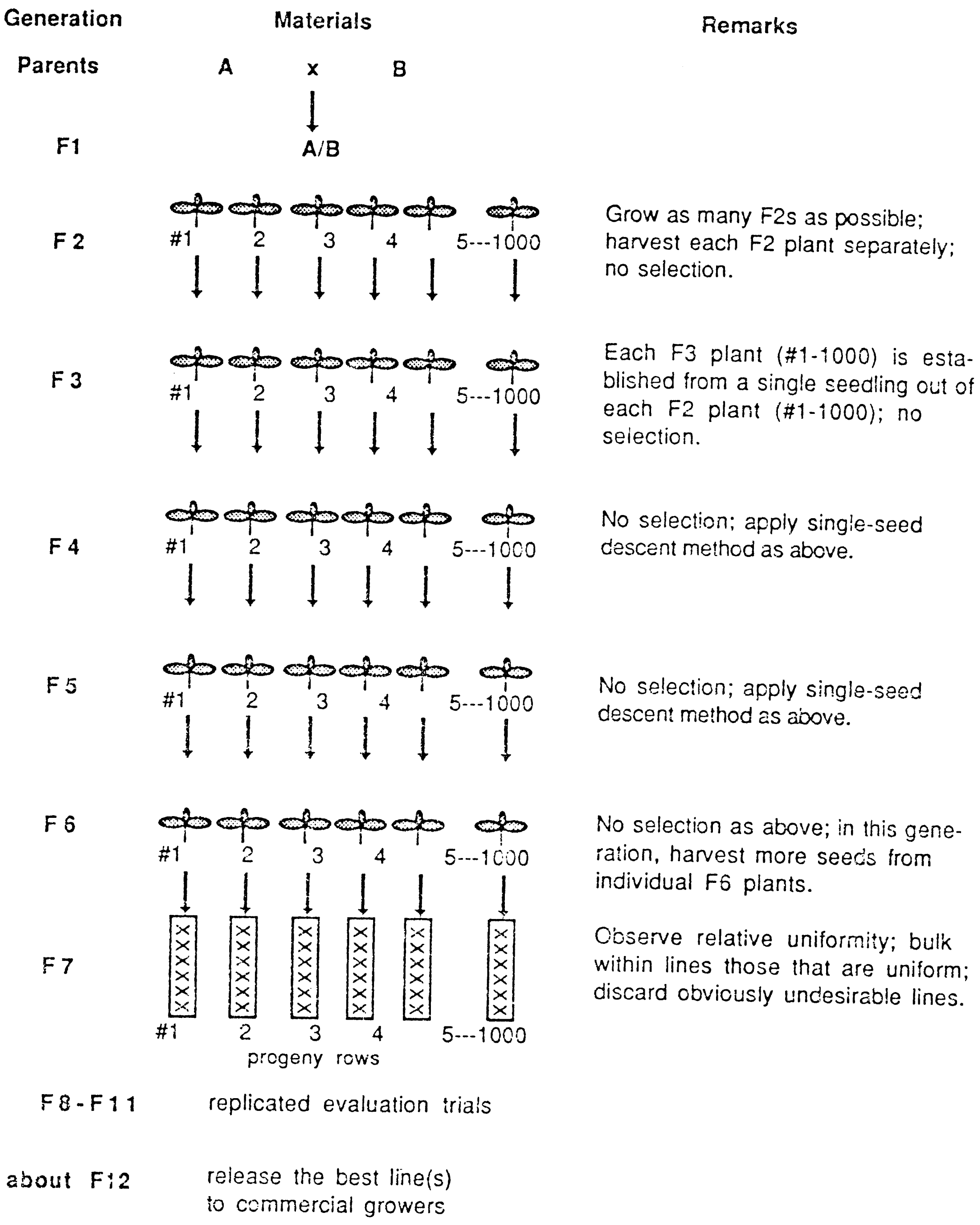

Figure 7. Diagrammatic sketch of the single-seed descent (SSD) method as applied to self-pollinated crops.

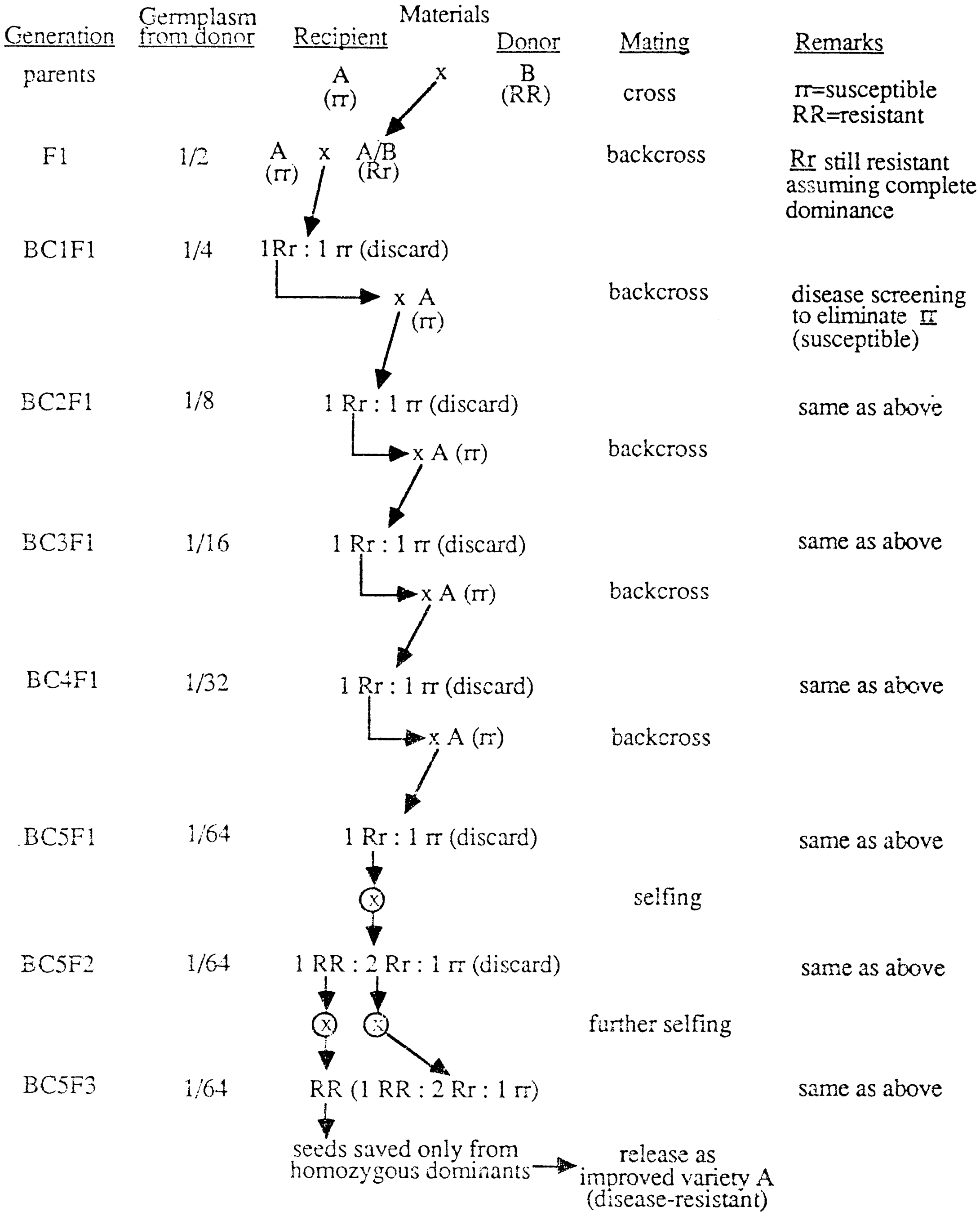

Figure 8. Diagrammatic sketch of the backcross method as applied to breeding for disease resistance, assuming single dominant gene control.

In every cross or backcross to the recurrent parent, the proportion of the genetic materials from the donor parent is reduced by one-half (1/2). In the F_1, this proportion is 1/2 or 50%. At the end of the 5th backcross, this proportion is only 1/64 or 1.6%. In other words, we would have recovered then approximately 98.4% of the genetic background of the recipient variety. If we designate the number of crosses and backcrosses to the recurrent parent as *b* , the proportion of germplasm from the donor parent is given by the formula:

$$\{\text{ Proportion of germplasm from donor parent} = (1/2)^b \}$$

Thus, after the initial cross (A/B) and 5 backcrosses, this proportion is $(1/2)^6$ or 1/64 or 1.6%.

The proportion of homozygosity and proportion of homozygous genotypes in any given backcross population are given by the same formula as that used in the selfing series, i.e.:

$$\{\text{ Proportion of homozygosity} = (2^m-1) / (2^m)\},$$

where m = number of backcross

and

$$\{\text{ Proportion of homozygous genotypes} = [(2^m-1) / (2^m)]^n \},$$

where m = number of backcrosses and
n = number of heterozygous loci in the F_1 of the original cross

Using the above formula, the proportion of homozygous loci in the BC_5 population would be $(2^5-1) / (2^5) = 31/32$ or 96.9%, which is similar for the selfing series. Under backcrossing, however, the homozygous loci would be those of the recurrent parent and are not different combinations of loci from both parents as they would be under the selfing series. This is because much of the original genes from the donor has been dissipated through the backcross series.

Assuming that 10 loci are originally heterozygous in the F_1 and that 5 backcrosses were made, the proportion of homozygous genotypes in generation BC_5F_1 would be: $[(2^5 - 1) / 2^5]^{10} = (31 / 32)^{10}$ or 72.8%. In other words, 72.8% of the BC_5F_1 population would be like the recurrent parent.

Backcrossing a character determined by a single dominant gene is relatively easy. As the example above shows, successive backcrosses (assuming a good selection regime is available to identify the gene under transfer) can be carried out without an intervening selfing series. It is only at the end of the backcross program that the progeny tests are done to identify the homozygotes.

With a recessive gene under transfer, it is necessary to grow the backcross generation to F_2 to identify the homozygous recessive genotype prior to making the next backcross. Alternatively, two or three successive backcrosses may be done but the second or third backcross should be grown to F_2 to find the homozygous recessives prior to the next round of backcrosses.

The method is very effective with simply inherited characters (high heritability). However, its use is not precluded for complex quantitative traits. The backcross generations need to be grown to F_3 in this case to effectively identify the most intense expression of the

trait under transfer, i.e. evaluation is on family basis rather than single plant performance. If heritability of the traits is low, the F_2 and F_3 populations will have to be large.

Backcross method offers the following advantages : previous gains are not lost because improvements are made in a stepwise fashion; the program may be independent of the breeder's target environment; evaluations of the backcross varieties may not be necessary; it is relatively rapid; it is predictable; and it is repeatable.

The one disadvantage of the method is that, apart from the gain provided by the additional gene (s) incorporated, there is a ceiling to the performance of the backcross derivatives imposed by the potential of the recurrent variety. In other words, the method does not create unusual gene combinations which may by better than the recurrent parent. This is absolutely why the recurrent parent must already be a successful variety. Nonetheless, the method can be modified in such a manner that enough backcrosses may be made to recover in large part the genetic materials of the recurrent parent and yet, leave enough variability for exploitation by other breeding methods such as bulk, pedigree or its combination.

Development of hybrid cultivars. Nowadays, it is not uncommon to find F_1 hybrid varieties of self-pollinated crops released for commercial production. Hybrid varieties were originally popularized among cross-pollinated crops such as maize but the idea has caught on among a number of self-fertilized crops, e.g. tomato, even though the evidences on heterozygote advantage ("heterosis") have not been unequivocal.

It is true that F_1 hybrids do exhibit favorable traits such as uniformity and to some extent, better resistance to diseases, but their advantages over the standard cultivars have not been as great as in cross-pollinating species. The popularization of F_1 hybrids among self-fertilized species owes much to the "biological" rights they impart to their developer (oftentimes, private seed companies). By releasing F_1 hybrids, nobody outside the company can duplicate them since they are the sole possessor of the parental stocks. This set-up gives private seed industries a certain measure of business security.

The development of F_1 hybrids in self-pollinated crops follows to a large extent the scheme used for cross-pollinated species. Usually, established varieties are intercrossed in some systematic fashion to find those that nick well (good combining ability) with each other. Thereafter, these parental stocks are "built-up" often in stepwise fashion to cure the possible defects of their hybrids. Such defects may be disease susceptibility, poor quality, etc. (though the combination itself may be high-yielding). The use of backcross method in improving the parental stocks is common. Once the improved parental stocks are available, the original combinations that nicked well are repeated (but now using the improved parents) to form the F_1 hybrid varieties.

As self-pollinated crops often do not have the mechanisms of hybridity that cross-fertilized species possess, e.g. self-incompatibility, male sterility, dioecy, etc., hybrid seed production is manually done. This activity takes invariably many hours of skilled work (depending upon species), inputs that usually translate into added seed cost. Thus, hybrid seeds among self-pollinated crops are almost always very expensive.

Future Developments

Tomato breeders have accomplished a great deal in the past. Important horticultural traits such as enhanced yield, disease and pest resistance, better quality for fresh consumption and for processing, adaptability to environmental stresses, adaptability to machine-harvesting and

to processing, and a host of others, have been bred into modern-day commercial cultivars. Despite all these improvements, tomato breeders have barely exploited the vast reservoir of genetic variability within the genus *Lycopersicon*. The building blocks for further improvement of tomato are clearly available and expanded efforts to conserve, evaluate and utilize this variability are crucial (Tigchelaar 1986).

Conventional breeding techniques are still expected to be the mainstay of most future breeding efforts to exploit the variability in cultivated and wild relatives of tomato. Additional improvements in the traditional techniques may be expected to facilitate the breeding process but, it is safe to say, that the limits of conventional breeding methods have, for the most part, already been reached. New vistas in genetically improving tomatoes will have to be explored. It appears that the promise of the new field of biotechnology will find early applications in tomato breeding.

The exploitation of biotechnological tools to enhance the improvement of tomato is rapidly gaining momentum in the developed countries. While these novel technologies may need time to mature and be adopted in real-life agricultural situations, their impacts are potentially revolutionary. Some aspects of biotechnology such as direct engineering of disease and insect pest resistance genes are bound to augment the work of the plant breeders to produce characters that were not previously existing. A good example is the recent engineering of a new tomato which does not become soft because the genetic code controlling the softening enzyme has been inverted and thus, "deactivated".

Of immediate applicability as an "enhancer" tool of plant breeding is the RFLP (restricted fragment length polymorphism) method. RFLP will likely be integrated into existing plant breeding programs allowing researchers to access, transfer and combine genes at a rate and precision never before possible (Tanksley *et al.*, 1989; Young and Tanksley 1989). Using RFLP, complex characters may be reduced to simpler genetic components thereby enabling an increasingly well-controlled breeding of cultivars with combinations of traits previously too difficult or time-consuming to breed for. Furthermore, the transfer of important genes from the wild relatives of tomatoes will be expedited by RFLP–future cultivars are expected to have enhanced yield, resistance to insects and diseases, better adaptability and improved quality.

With respect to tomatoes in the developing world, AVRDC research has successfully brought the crop to adapt reasonably well to the hot and humid lowland tropics. Advanced tomato breeding lines are now available that resist the major diseases such as bacterial wilt, tomato mosaic virus and nematode, are tolerant to the hot wet tropical conditions, and bear fruits that are firm, of improved size and resistant to cracking. While relief through the revolutionary methods of biotechnology may take a while before it percolates to the developing countries, what advances in conventional breeding programs, such as that at AVRDC[9], are in store for tomatoes in the tropics?

With increasingly pressured environments, tropical tomatoes of the future will have to carry tolerances to more stresses than ever. On the biotic constraints, AVRDC's tropical tomato research seeks advances not only in the levels of disease resistance but also in the range of diseases that the advanced breeding lines would be resistant to. Progress in breeding for resistance to the following diseases are expected: viruses such as potato virus Y and

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9 AVRDC is also now gearing towards gaining the full benefits of developments in the field of biotechnology, if not fundamentally, at least in the aspects of adopting proven methods that will enhance the Center's role in vegetable improvement for the developing countries.

leafcurl; other bacterial diseases such as bacterial spot; and certain fungal diseases like black leafmold (*Cercospora fuligena*). Even resistances to unwieldy viruses, such as CMV, and equally important insects like fruitworm and aphids, may be unravelled as the potential of hitherto unexploited wild *Lycopersicon* and *Solanum* germplasm is widely explored. Multiple resistances to biotic stresses will have to be a standard feature of future tropical tomatoes.

The ability to set fruits under hot humid conditions is a basic feature of tropical tomatoes. This physiological asset needs to be reinforced in future breeding lines. Heat tolerance (specific for hot dry condition) , drought tolerance, tolerance of excess soil moisture, and even tolerance of poor soil fertility may all have to be added into the physiological arsenal of future tropical tomatoes.

Apart from more and better stress tolerances, tropical tomatoes of the future will need a significant upgrading of quality, especially in the readily apparent parameters of fruit acceptability like absence of cracks, reduced blotchy ripening, improved color, and increased longevity in transit or storage through better fruit firmness and/or prolonged ripening behavior.

As the food technology industry in the Asian region continue to grow, there will be an increasing demand for processed tomato products. A significant fraction of this need will still depend on importation; however, some countries especially those still strapped of foreign currency reserves, are expected to continue exploring the development of their native tomato processing industry. These countries will need better technology for processing tomato production, not only to enhance productivity but also to improve processing quality. The tropical processing tomatoes of the future will have to be better adapted to the tropics than they currently are; more and better levels of disease resistance and better processing quality will be needed. In special circumstances, adaptability to mechanical harvesting may be a necessary feature.

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Genetics and Breeding of Potato with Special Reference to Some Breeding Problems in Developing Countries

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1. Introduction

Potato (*Solanum tuberosum* L.) is an ancient South American food staple which has spread worldwide and ranks among the world's major food crops along with rice, wheat and corn. Hawkes (1967; 1978) elegantly described the history of potato development and spread from the time it was moved from its center of origin, the Andean mountains of South America, to the present where it has gained the status of a principal foodstuff of great economic importance.

Relative to the cereals, potato is, by a large measure, a more remarkable crop because it combines two of the most important attributes of a staple food—high yield per unit area per unit time with a good balance of carbohydrates, protein and minerals. By itself, potatoes show a protein biological value of 98, a close second when compared to the reference protein of eggs at 100 (cf. Anon, 1980a). Its average energy production per day is second only to sweet potatoes and higher than rice, corn or cassava. Potato protein production per hectare per day is estimated at 1.3 kilograms, the highest among major tropical food crops. Its short growing period provides another advantage: at 125 days average, it is fast growing and can thus fit easily into most existing cropping systems.

The highest production levels on per capita basis are in the northern latitude countries of Europe and North America, and not surprisingly, these are the areas where the contribution of potato to human caloric intake is greatest. In recent years, production has declined in several West European countries mainly due to a gradual reduction in production areas (Horton, 1978). On the other hand, for the developing countries as a group potato production has grown at a faster pace than production of most other food crops (Fig. 1).

As a general trend in developing regions, potato yields have kept pace with the increases in cereal yields (Horton, 1987). Improvements in varieties, seed systems, and post-harvest technology have helped bring down the cost of producing potatoes in the developing areas. Indeed, the balance of world potato production is now gradually shifting from developed to the developing countries and from temperate to the tropical countries. The depressed potato yields in other areas of the developing world may be continually attributed to the persistently low levels of potato technology—poorly adapted cultivars, inavailability of clean seed, inadequate pest and disease control practices, lack of appropriate storage facilities, insufficient agronomic practices knowhow, etc. (Anon, 1976b).

It is not within the scope of this lecture to discuss the above problems but a brief reference to the aspects of cultivar development in developing countries is given here as a prelude to the main theme—genetics and varietal improvement of potato. Further discussions are given in later sections.

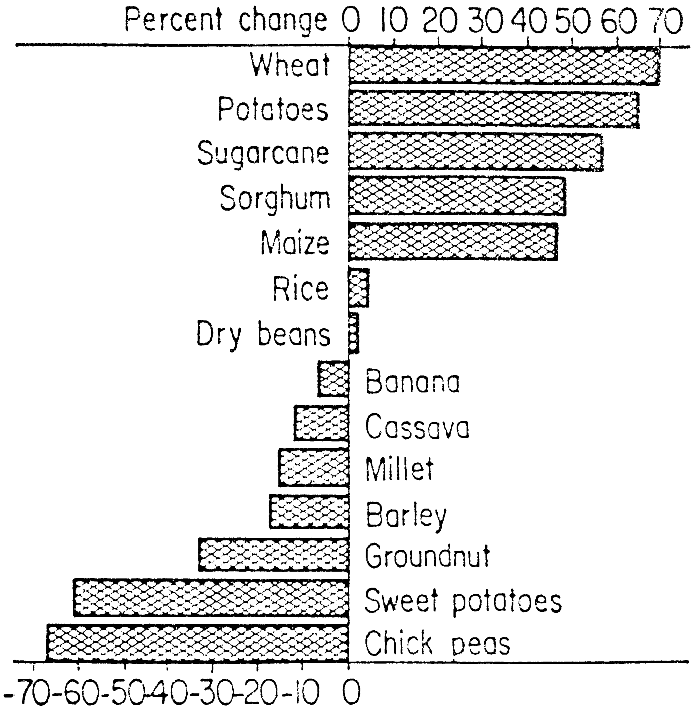

Fig. 1. Change in per capita production of major food crops in developing market economies, 1961/65-1982/84. Source: FAO, Production yearbook 1976; 1984 (Rome, 1977; 1985).

Most potato cultivars grown in developing countries were bred in the temperate zones. In the absence of any breeding program to serve the local variety requirements, there is simply no recourse but to find the most suitable types from among introduced cultivars. The climatic conditions of the temperate regions are however far different from those in developing countries (especially in the tropics where most of these countries lie)—variations in daylength, temperature, rainfall and other abiotic factors are very pronounced. Logically therefore, the varieties from temperate countries are generally unadapted when grown in the tropics even if the temperature stress is significantly reduced by concentrating production in the cooler highlands.

Several developing countries of the Asian region have had, or are now interested on varietal improvement programs. As a matter of fact, countries such as Indonesia, Philippines, Thailand, Sri Lanka, and Papua New Guinea have established a regional cooperative linkage under the aegis of SAPPRAD (Southeast Asian Program on Potato Research and Development). In this, potato breeding to serve the needs of member countries is an important component. The role of the International Potato Center (CIP) in terms of availing improved germplasm (but not named cultivars) should significantly improve the chances of finding better adapted varieties for the tropical countries.

It is therefore the objective of this article to provide tropical potato breeders with sufficient background information relevant to potato breeding and consequently, to present

the various techniques of breeding, traditional and unconventional, which have been practised or are currently being explored. In the process, it is hoped that the body of information presented herein will provide some useful guidelines.

2. Biosystematics of Potato and the Range of Exploitable Diversity

Much of the breeding in potato since it was brought into Europe in the early 16th century has been simply a continuous reassortment of the variability contained in the few, original Andigena introductions. Still, the evolution of subspecies Tuberosum from those limited introductions through the combined forces of natural and human selection (Salaman, 1964; Salaman and Hawkes, 1949; Salaman, 1954; Hawkes, 1967) is a remarkable proof to the enormous store of genetic variation that those clones carried. There were only a few occasions in the past when genetic diversity had been significantly added to the present day Tuberosum gene pool, such as the importations of new Andigena germplasm into New York by Rev. Chauncey Goodrich between 1848 to 1852. Rough Purple Chile, one of those clones imported from Panama, figured in the pedigree of many later varieties by way of its descendant, Early Rose.

Overall, the progress that has been attained by the 19th century potato breeders was made on a very narrow genetical base (Simmonds, 1969). When further decimation of the gene pool by the late blight epidemics of the 1840's is taken into account, it becomes even more remarkable that the limited genetic materials have been extremely rewarding and this must be due in large part to the variability concealed by heterozygous clones.

It is reasonable to assume that the diversity contained in the original Andigena introductions into Europe is but a small portion of what existed at the Andean center of origin even if recorded introductions are taken as only a token of the actual number (Cardenas, 1966). Roughly, less than one percent of the genetic variability of *solanum* has been utilized in the development of existing varieties of potatoes (Anon, 1974). A brief biosystematic treatment of the potato should serve to stress the above point as well as emphasize the fact that an enormous range of genetic diversity is indeed available for potato breeders to exploit further.

The potato of commerce that we all know belongs to *Solanum tuberosum* L., one of eight cultivated species. Apart from the cultivated species, 154 wild species of potato are recognized (Hawkes, 1978). The rest of the genus *Solanum*, an extremely large genus comprising of some 2,000 species, are non-tuber bearing forms (although two non-tuber bearing series, *Juglandifolia* and *Etuberosa*, are included under Section Petota to which the potato species belong on the basis of key morphological traits).

Table 1 shows the recognized series under Section Petota, the number species within each series, the chromosome races when available, and traits that have so far been identified in some of the better known species. The limited information concerning valuable traits of some species given by Hawkes (1978) were supplemented with those provided by Anon (1974). Additional information, where specifically sought, may be obtained from Bulletin 533 of the College of Agriculture and Life Sciences, University of Wisconsin, Madison, Wisconsin 53706, U.S.A., entitled "Inventory of tuber-bearing *Solanum* species" by Ross and Rowe (1966). This bulletin is very useful in listing sources of resistance to a number of diseases, where known, in the IR-1 potato Collection in the United States.

As may be noted, 18 series are recognized of which series Tuberosa is the largest. Series Tuberosa itself is further subdivided into cultivated and wild species. The cultivated forms occur at four ploidy levels, tetraploids being the major cultivated group. The frost-resistant species, *S. ajanhuiri*, *S.* x *goniocalyx* (*x* indicates species hybrid form) and *S.* x *curtilobum* are grown at 3,000 to 4,000 m above sea level in the Andean mountains of South America. *S. tuberosum* ssp. *andigena*, *S. stenotomum* and *S. goniocalyx* are mostly grown at 2,500 to 3,500 m. *S. phureja* , on the other hand, are well adapted to the warm temperate frost-free lower valleys of the eastern Andes. As cited earlier, *S. tuberosum* ssp. *tuberosum* evolved from ssp. *andigena* by human and natural selection forces to adapt them to long days in lower altitudes of higher latitude regions of the world and to some extent, although not considered fully well-adapted, to higher altitudes in tropical countries.

In comparison to the cultivated species, wild species thrive in a wider range of habitats and have a broader latitudinal distribution. Apart from their greater climatic adaptability, wild species generally show greater adaptation to pests and diseases oftentimes lacking among the cultivated forms, Their potential value in breeding has not been fully exploited however. Nonetheless, a few outstanding examples of their useful contribution to the *tuberosum* gene pool are already known—major R-genes for late blight resistance from *S. demissum*, resistance to PVY from *S. stoloniferum* and *S. chacoense*, and frost resistance from *S. acaule*. There are of course still a great number of important traits that remain untapped (see Table 1). The breeders apathy towards the use of wild species for breeding purposes is not entirely unfounded (see section 5.1.4.2). In some cases, breeding barriers between cultivated and wild species do exist although, as a whole, they are known to hybridize well enough so that enforcing the gene flow from many wild species to the cultivated types is not an impossible task. Majority of wild diploid species will hybridize easily with cultivated diploids. Even tetraploid x diploid crosses can be accomplished, although with slight difficulty.

Hawkes(1978) cited several forms of interbreeding barriers in natural populations: temporal barriers such as difference in flowering time between two species with overlapping ecological distribution; clear cytogenetical barriers resulting in F_1 hybrid sterility; and F_2 hybrid breakdown giving rise to F_2 plants of low fertility and viability. In general, there are two main groups of potato which are difficult to cross. The first group includes the series Morreliformia, Bulbocastana and Pinnatisecta. The second consists of series Commersoniana, Circaeifolia, Conicibaccata, Piurana, Acaulia, Demissa, Longipedicellata, Cuneoalata, Megistacroloba and Tuberosa. Thus far, there have been demonstrated instances where, through proper manipulations such as the use of bridging species, hybridization barriers between certain species from the two groups have been broken (Dionne, 1963; Hermsen and Ramanna, 1973). Hawkes (1978) predicted that most, if not all, of the wild potato species (with the probable exception of non-tuberiferous series Juglandifolia and Etuberosa which lie outside any of the potato crossability groups) will sooner or later be brought into the gene pool of the cultivated potato, *S. tuberosum*. If such is the case, the already large gene pool will further expand thereby increasing the range of exploitable diversity available to the breeders.

Table 1. Biosystematic groupings in the genus *Solanum* Section Petota, chromosome numbers, and some recognized valuable characters of a few well-known species (modified after Hawkes, 1978)

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
I. JUGLANDIFOLIA (non-tuber bearing)	- *juglandifolium, lycopersicoides, ochrantum, rickii*	24	not well-studied
II. ETUBEROSA	- *etuberosum, brevidens, fernandizianum*	24	not well-studied
(non-tuber bearing)	- *palustre, subandinum*	?	*palustre* rare or extinct
III. MORRELIFORMIA	- *morreliforme*	24	not well-studied
IV. BULBOCASTANA	- *bulbocastanum* (3 subspecies)	24,36	resistance to late blight and leafhopper
	- *clarum*	24	not well-studied
V. PINNATISECTA	- *brachistotrichum, michoacanum* (sp. hybrid), *stenophyllidum*	24	not well-studied
	- *cardiophyllum* (3 subspecies), *jamesii*	24,36	resistance to late blight in *cardiophyllum*
	- *hintonii, nayaritense*	?	not well-studied
	- *sambucinum* (sp. hybrid), *trifidum, pinnatisectum*	24	resistance to late blight in all species; leafhopper resistance in *pinnatisectum*
VI. COMMERSONIANA	- *yungasense* (2n =24), *calvescens* (2n=36)	24,36	not well-studied
	- *tarijense*	24	resistance to late blight, early blight, *Verticillium* wilt, aphids
	- *chacoense* (2 subspecies)	24	resistance to virus Y, blackleg, early blight, *Verticillium* wilt, cyst nematode (?), aphids, Colorsdo beetle
	- *commersonii* (2 subspecies)	24,36	moderate frost resistance, some resistance to late and early blight
VII. CIRCAEIFOLIA	- *capsicibacatum, circaeifolium*	24	not well-studied
VIII. CONICIBACCATA	- *agrimonifolium, colombianum, longiconicum, oxycarpum*	48	not well-studied

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	- *albornozii, ayacuchense, buesii, multiflorum, paucijugum, pillahu-atense, tundalomense, urubambae, villus-petalum, woodsonii*	?	not well-studied
	- *moscopanum*	72	not well-studied
	- *chromatophilum, jae-nense, laxyssimum, neovargasii, viola-ceimarmoratum*	24	some frost resistance in *chromatophilum*; others not well-studied
IX. PIURANA	- *solicii, yamobambense*	?	not well-studied
	- *agrolossum, paucissec tum, piurae*	24	not well-studied
	- *tuquerrense*	48	self-incompatible tetraploid
X. ACAULIA	- *acaule* (4 subspecies)	48,72	resistance to ring rot, high frost resistance, some resistance to late blight and cyst nematode (?)
XI. DEMISSA	- *brachycarpum, iopetallum*	72	not well-studied
	- *demissum, guerroense, hougasii*	72	late blight resistance in all but especially *demissum* (also carries PVY and leafhopper resistance); PVY resistance in *hougasii*
	- *edinense* (sp. hybrid; 2 subspecies), semidemis-sum (sp. hybrid ?)	60	resistance to late blight
XII. LONGIPEDICELLATA	- *fendleri* (2 subspecies), *jertingii, papita, polytri chon, stoloniferum*	48	late blight resistance in *stoloniferum* and *polytrichon*; virus resistance in *fendleri* and *stoloniferum* (also flea beetle resistance)
	- *vallis-mexice* (sp. hybrid)	36	not well-studied
XIII. POLYADENIA	- *lesteri, polyadenium*	24	resistance to late blight and aphids in *polyadenium*
XIV. CUNEOALATA	- *infundibuliforme*	24	possible drought resistance

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	- *anamotophilum*	?	possible drought resistance
XV. MEGISTACROLOBA	- *chavinense, hastiforme, toralapanum*	24	not well-studied
	- *dolichocremastrum, hawkesii, huanocense*	?	not well-studied
	- *boliviense, megistacrolobum, raphanifolium, sanctarosae, sogarindinum*	24	frost resistance in all species; also resistance to cyst nematode in all except *raphanifolium* and *sogarindinum*
	- *bruecheri* (sp. hybrid)	36	not well-studied
XVI. INGAEFOLIA	- *ingaefolium*	?	not well-studied
	- *rachialatum*	24	not well-studied
XVII. OLMOSIANA	- *olmosense*	24	not well-studied
XVIII. TUBEROSA			
a. Wild Species	- *abancayense, alandiae, amabile, ambosinum, andreanum, brevicaule, cajamarcense, coelostipetalum, colominense, cyanophyllum, doddsii* (sp. hybrid), *jalcae, lobbianum, minutifolium, mochicense, mollepujroense, orophilum, paramoense, regularifolium, rhompodeilanceolatum, sandemanii, scabrifolium, suffrutescens, torrecillasense, trinitense, velardei, virgultorum*	?	cyst nematode resistance in *andreanum* and *brevicaule*; frost resistance in *jalcae*; *others* not very well-studied
	- *berthaultii* (sp. hybrid), *bukasovii, canasense, candolleanum, cantense, chancayense, chiquidenum, contumazaense, gandarillasii, gracilifons, huncabambense, humetophilum, hypacrarthum, immite, kurtzianum, lepthophyses, lignicaule,*	24	aphid resistance in *berthaultii*; cyst nematode resistance in *kurtzianum, leptophyses, multidissectum, spegazinii, sparsipilum, vernii*; frost resistance in *bukasovii, canasense, multidissectum, spegazinii*, vernii;

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	marinasense, multidissectum, multiinterruptum, neoweberbauri, pampasense, pascoense, rechei (sp. hybrid), *setulosistylum, spegazinii, sparsipilum, vernii, verrucosum, vidaurrei, weberbaueri, wittmackii*		late blighy resistance in *kurtzianum, spegazinii, vernii, verrucosum*; drought resistance in *gandarillassii, kurtzianum, sparsipilum*; blackleg resistance in *setulosistylum*; others not well-studied
	- *maglia, microdontum* (2 subspecies), *medians, venturii)*	24,36	resistance to cyst nematode in *venturii* and *microdontum* (also to PVY and late blight)
	- *acroscopium, sucrense*	48	resistance to cyst nematode in *sucrense*
	- *goularyi*	24,48	not well-studied
	- *oplocense*	24,48,72	resistance to cyst nematode
b. Cultivated pecies 1. Diploids	- *ajanhuiri, goniocalyx, phureja, stenotomum*	24	frost resistance in *ajanhuiri, goniocalyx*, and some in *stenotomum* ; resistance to bacterial wilt, *Verticillium* wilt, blackleg, and late blight in *phureja*
2. Triploids	- *chaucha* (sp. hybrid), *juzepcaukii* (sp. hybrid)	36	immunity to virus X and wart, late blight resistance, high dry matter and protein in *chaucha*; resistance to wart, hypersensitivity to virus X, resistance to frost, early blight and cyst nematode in *juzepczukii*
3. Tetraploids	- *tuberosum* (ssp. *tuberosum, andigena)*	48	*tuberosum* is the cultivated form in most areas of the world except South America where the *andigena* form is grown; many important traits of commercial

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
			significance already in *tuberosum*; some resistance to late blight, immunity to PVY, resistance to PVX, PVS, common scab, wart, *Verticillium* wilt, aphids, leafhoppers, cyst nematode, root knot nematode, etc, in ssp. *andigena*
4.Pentaploids	- *curtilobum* (sp. hybrid)	60	some frost resistance; resistance to late blight, wart, early blight, *Fusarium*, high dry matter and high protein

3. Reproductive Systems of Potato: Consequences in Breeding and Production

The breeding system of a particular species largely dictates the breeding methods to be used (Table 2). Even within a defined system, breeding approaches may vary in accordance with the primary objectives of the plant breeder and / or the nature of the parents chosen in a hybridization program. For example, backcross breeding is more appropriate than other methods when one of the parents (usually termed the donor) is a commercially undesirable type but carrying an important trait lacking in the other parent (usually termed the recipient or recurrent parent), normally a popular cultivar. .

Potato reproduces both sexually and vegetatively (via tubers). The sexual system affords the plant breeder with a reliable scheme to generate variability from which new cultivars may be derived. It has been through this system that most, if not all, present day cultivars had been and still are being produced. Bud sports arising through somatic mutations have, on several occasions, improvement of potato is rather small (Van Harten, 1978).

Most diploid potato species (both cultivated and wild) are outbreeders. This mating system is obligatory because of the presence of a genetically controlled self-incompatibility mechanism. The incompatibility is of the gametophytic type and, as in many other crop plants exhibiting the same system, due to a series of S-alleles. Self-compatible species such as *S. brevidens*, *S. etuberosum* and *S. morreliforme* provide exceptions to the usual rule of self-incompatibility among diploid species (Hawkes, 1978).

In contrast, most pollen-fertile tetraploid and hexaploid species are self-compatible. The presence of S-alleles among cultivated tetraploids (sub-species *tuberosum* and *andigena*) has been proved by investigations of dihaploid derivatives (Cipar, Peloquin and Hougas, 1964). Although self-pollination is possible, the cultivated tetraploids still behave basically as outbreeders and exhibit inbreeding depression upon selfing. Krantz (1946) studied the effect of inbreeding on tuber yield and reported a 17% yield reduction in the first (I_1) inbred

generation. By the I_6 generation, the actual yield of the inbred family was only 19% relative to the mean F_1 performance.

The breakdown of the self-incompatibility mechanism at the higher ploidy levels in potato has been suggested to be due to competitive interaction (or mutual weakening) of S-alleles. This theory was advanced by Lewis (1954) and further supported by Arasu (1968). Cipar (1964) found however a high incidence of self-compatibility among normally self-incompatible hybrids of dihaploids with *S. phureja*, implying that the self-compatibility in cultivated tetraploids is due to genes modifying the action of S-alleles rather than competitive interaction. Although belonging to another species, *S. tuquerrense* in the series Piurana is a curiously self-incompatible tetraploid and provides an exception to the self-compatibility rule in the tetraploid group (Hawkes, 1978). Moreover, its maintenance of incompatibility at the polyploid level does not conform with the theory of competitive S-alleles interaction.

Several important consequences of vegetative propagation in potato breeding were given by Howard (1970; 1978). Asexual propagation allows maintenance of the genetic identity of individuals barring rare somatic mutations. Therefore, every seedling in the breeding program can be a potentially new variety. The use of other methods such as wide crosses, mutation breeding, and polyploidy breeding is similarly facilitated by asexual propagation. Any promising individuals therefrom can easily be maintained and/or propagated.

Asexually-propagated crop species are generally highly heterozygous. Potato is not an exception. When two cultivars are crossed, segregation for a wide array of traits is immediately apparent in the hybrid seedlings. While this condition provides breeders with a slight temporal advantage, selection at least for some traits being possible in the F_1 generation, the genetic consequence of heterozygosity far outweighs the time gained. The highly heterozygous nature of potato cultivars means that, when hybridized among each other, they can transmit their good characteristics only to a very small proportion of the progenies. Therefore, growing a large number of hybrid progenies is an absolute prerequisite to maximize the chances of isolating desirable recombinants.

Debilitating virus diseases usually accumulate in vegetatively propagated crop plants especially if no measures are taken to minimize virus infection. Degeneration of potato varieties is a well-known problem. Fortunately, virus-infected cultivars can now be routinely "cleaned" by meristem culture methods (Morel, 1964; Kassanis, 1965). However, such procedures are ineffective unless combined with good seed production practices such as the use of appropriate seed districts, efficient pest and disease management, effective seed certification scheme, etc. Virus diseases, except potato spindle tuber viroid (Diener, 1971), are non-transmissible by true seeds. Every new seedling therefore arising from true seeds is practically virus-free and it is the responsibility of breeders to insure that they remain so through the different stages of selection and clonal multiplication. Unless this is kept in mind, valuable genotypes could easily be selected against on account of virus-infection.

Other disadvantages to the breeder accruing from the vegetative reproduction of the potato (Howard, 1978) are as follows:

(a) varieties may not flower or even if they do, could be pollen sterile (ovule sterility is rare) and therefore, their use is restricted in the crossing programs;
(b) large amounts of materials must to be stored under ideal conditions;
(c) transport of tubers is much more difficult than that of seeds;
(d) clonal materials do not store as easily as seeds and must be grown each year ;
(e) multiplication rate is much slower than by seeds.

Table 2. Genetic architectures and breeding methods applied to different breeding systems (partly modified from Briggs and Knowles, 1967)

Characteristic or Breeding Technique	Breeding System		
	Self-pollinating species	Cross-pollinating species	Facultative asexual
a. GENETIC ARCHITECTURE OF NATURAL POPULATIONS			
Genotype of the sporophyte	homozygous	heterozygous	heterozygous
Genotype of the gametes from a single plant	similar	different	different
Progeny of a single plant	homogeneous	heterogeneous	heterogeneous
Self-incompatibility	none	frequent	yes
Inbreeding depression	none	usual	yes
b. BREEDING TECHNIQUE			
Introduction	yes	yes	yes
Pure line selection	often	only as parents for hybrid varieties	proposed for creating hybrids but not fully developed
Mass selection	occasionally	frequently	occasionally for population improvement
Pedigree breeding	yes	no	yes, but not in the context of the method as applied to self-fertilizing species
Backcross breeding	yes	yes	yes (modified method)
Hybrid varieties	occasionally	yes	proposed but not fully developed
Recurrent selection	occasionally	yes	occasionally for population improvement

[a] Using cultivated potato tetraploids as example; facultative asexuals are species which normally reproduce vegetatively but capable of sexual reproduction, e.g., potato.

Another obvious disadvantage of vegetative propagation may be added to the above—the constant fear of introducing tuber-borne viral, fungal and bacterial diseases, and pests (including nematodes) constitutes a serious deterrent to free germplasm exchange among breeding programs. The use of tissue culture (Roca *et al.*, 1979) may alleviate this problem and enable a more widespread transfer of potato genetic materials especially those coming

from South America, the widespread transfer of potato genetic materials especially those coming from South America, the recognized center of diversity.

4. Genetic Basis of Some Morpho-Physiological Traits and Resistance to Diseases

Howard (1970) reviewed previous works in potato genetics with emphasis on the cultivated tetraploids. In addition, previous surveys have been done, all published in the journal "Bibliographia Genetica": Fruwirth (1925) in Vol. 1 pages 315-362; Swaminathan and Howard (1953) in Vol. 16, pages 1-192; and Howard (1960) in Vol. 19, pages 87-216.

This section is largely a summary of information provided by Howard (1970) but supplemented by more recent literatures whenever available. It must be understood that there are many gaps in our knowledge of potato genetics primarily because potato is not an ideal specimen for genetical research—it is a tetraploid which introduces some complexity to interpretation of genetic data; moreover, potato has a large number of small chromosomes; it is rather bulky and requires considerable expenditures of land or greenhouse space to raise an adequate population size; being propagated vegetatively, it also becomes too quickly infected by degenerative viral diseases.

The advent of dihaploids (haploids derived from tetraploids) should greatly facilitate genetic studies because of the relative genetic simplicity at this ploidy level. Genetic stocks are also being used to establish linkage relations and in crosses with trisomics to situate genes to particular chromosomes (Hermsen *et al.*, 1973). These trisomic sets have already been established in *S. tuberosum* (Yeh and Peloquin, 1965; Ramanna and Wagenvoort, 1976). Therefore, the future has in store the filling up of gaps in our knowledge of potato genetics.

4.1 Tuber flesh, stem, and sprout pigmentation

Anthocyanin pigments in potato are found in flowers, stem, sprout and in some cases, in flesh as well as skin of tubers. At least six major genes controlling anthocyanin pigmentation in tetraploid cultivated potatoes are known (Salaman, 1926; Sirks, 1929; Asseyeva and Nikolayeva, 1935; Lunden, 1960; Howard, 1970). Four of these genes, designated by symbols R, E, D, and P, act independently in controlling sprout pigmentation. Nearly all varieties have one or more of the four genes and therefore, it is very infrequent to find unpigmented sprouts. These same four genes may be involved in the control of stem color.

Krantz (1922) concluded that purple flesh of cv. Congo Black was due to a single dominant gene based on the 3:1 purple to white fleshed ratio among its selfed progenies. A more complicated situation was observed by Muller (1923) who observed a 9 pigmented : 7 white ratio upon selfing a pigmented variety. Only white fleshed types resulted in crosses with a white variety. Complementary genes C and I were postulated for flesh color along with an inhibitor, gene Z.

4.2 Tuber shape

Salaman (1926) suggested that tuber shape was conditioned by a single gene for length. Long shape was dominant to round tubers which bred true to type. Bartosch (1930), Rathlef and Siebeneck (1934), and more recently Schick (1956) disagreed with the single gene theory and suggested instead that several genes are likely involved to explain the distribution of shapes in segregating families studied.

4.3 Depth of eyes

Although there was no complete dominance among hybrid progenies, deep eyes was largely dominant to shallow eyes (Salaman, 1912; Heribert-Nilsson, 1913). East (1910) and Black (1930) suggested otherwise and postulated a genetic control by more than one gene. According to Huber (1930), two complementary genes were involved in shallow eye expression.

4.4 Tuber flesh color

Deep yellow flesh was found to be dominant to white and controlled by a single gene and modifiers with small effects (Fruwirth, 1912; Salaman, 1926). Schick (1956) and Engel (1957) agreed with this theory although certain findings such as those by Heribert-Nilsson (1913) and Black (1930) seemed to refute the early theory.

4.5 Growth habit

At least three genes are involved in the genetic control of growth habit, with normal upright dominant over prostrate (Salaman and Lesley, 1920). Procumbent (intermediate between extremes of growth habit) was recessive to upright and monogenically controlled.

4.6 Glycoalkaloids

The inheritance of major glycoalkaloids, the bitter principle in tubers of wild potato, *S. chacoense*, identified by thin-layer chromatography, has been studied (McCollum and Sinden, 1979). Monogenic segregations (3 : 1 in F_2 and 1 : 1 in BC_1) were obtained for presence : absence of glycoalkaloids solanine, chaconine, and commersonine. In simultaneous segregation of the three glycoalkaloids, the following interpretations were suggested to explain the observed results:

(a) solanine and commersonine are determined by alternative co-dominant alleles at a single locus;
(b) the major gene for chaconine segregates independently of the sola nine/commersonine locus;
(c) a recessive gene linked with commersonine allele was epistatic to the chaconine gene causing production of b-chaconine instead of the usual a-chaconine.

The F_2 fits the ratio 3 : 6 : 3 : 1 : 2 : 1, seen as combining the 1 : 2 : 1 segregation of solanine : solanine + commersonine : commersonine and the 3 : 1 segregation for presence : absence of chaconine.

4.7 Tuber number, size, yield and time to maturity

These characters are lumped here because as major components of yield, number and size of tubers, and growth duration are highly influenced by daylength. For example, tuber initiation is earlier under short days than under long days and tuber yield in relation to weight of haulm (vegetative portion) is much higher under short days. Maturity is also shortened under short days. It is therefore important to realize that any results on inheritance of time to maturity and yield must consider the large influence of photoperiod (Howard, 1970).

Engel (1957) studied tuber number, size and yield, and concluded that yield is difficult to determine for large number of seedlings, even if difference in maturity and environmental responses are disregarded. The accuracy of yield determinations depends on large samples, determination based on single plants having an extremely high error.

Schick (1956) and Moller (1956) studied the frequencies of early maturing seedlings under long day conditions from crosses of two early maturing varieties and concluded that maturity depends upon a number of genes and varieties are heterozygous for most of these.

4.8 Resistance to late blight

Late blight, caused by *Phytophthora infestans* (Mont.) de Bary, attacks both the foliage and the tubers. A typical symptom on the leaves is shown in Figure 2 below:

The hypersensitive type of foliage resistance to late blight, controlled by R-genes, has been widely studied. The main source of this type of resistance is the wild Mexican hexaploid species (2n = 72), *S. demissum*. To date, 11 major R-genes are known.

Major R-gene resistance is race-specific and very unstable in the face of a highly variable pathogen (Section 5.1.4.7.1.). Black *et al.* (1953) established the relation between the genes for hypersensitivity and the races of the pathogen. The scheme is internationally accepted and based from the original work of Black (1952). A sample of this nomenclature is given in Table 3.

The hypersensitive resistance type is considered of limited importance because of its instability. As new resistance genes and their combinations are bred, it does not often take long for new races capable of attacking them to arise. Greater interest is now focused on another type of resistance called field resistance or non-race specific resistance. In theory and practise, this type of resistance is more longer - lasting than race-specific resistance. Black

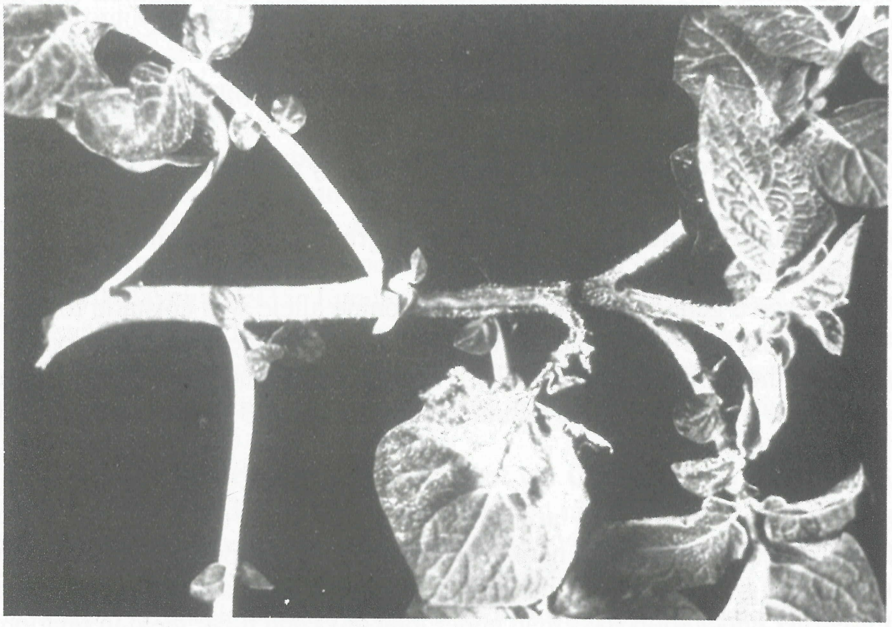

Fig. 2. Typical late blight symptoms on potato leaves.

(1960; 1972) suggested that field resistance is controlled by many genes (see Table 7). Sources of this type of resistance have been found also in *S. demissum* and other species, both cultivated and wild (section 5.1.4.7.1).

Table 3. A sample of the international scheme on nomenclature of major R-genes for resistance and races of *Phytophthora infestans* (after Black et al., 1953).

Potato genotype	Phyisiological race of *P. infestans* [a]							
	0	1	2	3	4	1,2	1,3	1,4
r	S	S	S	S	S	S	S	S
R_1	R	S	R	R	R	S	S	S
R_2	R	R	S	R	R	S	R	R
R_3	R	R	R	S	R	R	S	R
R_4	R	R	R	R	S	R	R	S
R_1R_2	R	R	R	R	R	S	R	R
R_1R_3	R	R	R	R	R	R	S	R
R_1R_4	R	R	R	R	R	R	R	S

[a] R = resistant; S = susceptible

4.9 Resistance to bacterial wilt

Bacterial wilt is caused by *Pseudomonas solanacearum* E.F. Smith. Figure 3 shows an infected potato plant. Resistance has been identified in *Solanum phureja* although apparently not common (Thurston and Lozano, 1968). Reaction to the pathogen at the diploid level appears to be conditioned by three dominant and independent genes plus modifiers (Rowe and Sequeira, 1970; Rowe *et al.*, 1972). At the tetraploid level, two dominant genes have been postulated to confer resistance (Anon, 1979). In addition, a dominant gene for susceptibility which exerted a dosage-dependent epistatic effect on the two dominant resistance genes was also suggested by the tetraploid segregation data. The dominant resistance genes were probably identical to those identified in *S. Phureja* (Opeña *et al.*, 1979; unpublished). It is possible to transfer the resistance from *S. phureja* to *S. tuberosum* (Gonzales *et al.*, 1973) but the degree of resistance varied with the virulence of the bacterial race.

Fig. 3. A potato plant showing symptoms of bacterial wilt infection.

Robinson (1968) provided evidence of the existence of two resistance forms: race-specific or vertical resistance and non-race specific or field resistance. Some clones had both types of resistance. As with late blight, vertical resistant genotypes showed signs of instability vis-a-vis the pathogen.

4.10 Resistance to virus diseases

Resistance to virus diseases in potato that are important from the breeder's standpoint falls under three categories: resistance to infection, hypersensitivity, and extreme resistance. Another form of reaction (termed "tolerance") to viruses in which the variety is less sensitive and shows only mild symptoms with slight or no yield reduction is also known. Breeding for virus tolerance however is not preferred.

Resistance to infection denotes the difficulty with which a variety becomes infected when exposed to the virus. Hypersensitivity implies extreme sensitive reaction that the virus is localized at the site of infection and no systemic infection occurs (Murphy, 1936). Extreme resistance is equivalent to immunity. This form of resistance was first identified by Schultz and Raleigh (1933) in a seedling that was resistant to PVX even after graft-inoculation.

4.10.1 Potato leafroll virus (PLRV)

As the name implies, the virus elicits upward rolling or cupping of potato leaves (Fig. 4). Not much is known about the genetics of PLRV resistance but many breeders suggest that it is likely polygenic. Resistance can be increased by intercrossing resistant types but is decreased when crossed with susceptibles. Sources of resistance have been identified in *S. tuberosum*, *S. demissum*, *S. andigena*, *S. acaule*, *S. stoloniferum* and *S. chacoense* (see also Table 1).

Fig.4. A potato plant infected with PLRV. Note upward cupping of leaflets.

4.10.2 Potato virus X (PVX)

High levels of resistance (hypersensitivity and extreme resistance) to PVX (see Fig. 5) are known. Resistance to infection is also available in some commercial cultivars and very likely polygenically conntrolled.

Hypersensitivity is conditioned by a single dominant gene inherited in tetrasomic fashion (Cockerham, 1943). Strain groups of PVX have been differentiated (Cockerham, 1955) by using varieties carrying no resistance (genotype n_xn_b), either one of the two resistance genes (N_xn_b or n_xN_b) and both (N_xN_b). Hypersensitivity was tested by graft inoculation which usually leads to a top necrosis reaction, a more reliable criterion than local lesion. Table 4 shows the interrelationship between the genes for hypersensitivity and strain groups of PVX. Hypersensitivity to PVX and PVX^B is determined by genes N_x and N_b, respectively. PVX^B is a strain of PVX.

Fig. 5. Common mosaic symptoms on potato leaves caused by PVX.

Table 4. Interrelationship of genes for hypersensitivity and strain groups of PVX (after Cockerham, 1955).

Variety	Genotype	Strain Group[a]			
		1	2	3	4
Arran Banner	n_xn_b	S	S	S	S
Epicure	N_xn_b	R	S	R	S
Arran Victory	n_xN_b	R	R	S	S
Craigs Defiance	N_xN_b	R	R	R	S

[a]R = hypersensitive; S = susceptible

Of the four strain groups, Group 3 is the most common and economically, the most important. Common strains of PVX belong to this group. Group 4 strain which is the most dangerous has not been found in commercial potatoes and only one strain has been described in the literature so far (Wiersema, 1972). Identification of reaction to Group 4 is usually done by grafting PVX^B -infected scions onto N_xN_b cultivars (Cockerham and Davidson, 1963; Rozendaal, 1966). Presumably, PVX^B mutates easily into a Group 4 type to infect all known N_xN_b varieties. Strains of Group 3 can also be obtained by grafting PVX^B scions onto n_xN_b varieties. PVX^B strain belongs to Group 2.

The drawback of hypersensitivity to PVX is that resistance is race-specific. Lessons from other crop diseases (rusts of cereals or late blight of potato) suggest that this type of resistance is unstable. Varieties carrying gene N_x have been grown for more than a century, however, without resistance-breaking strains arising (Wiersema, 1972). Hypersensitivity still seems to be a valuable form of resistance in potato breeding.

Immunity to PVX was first discovered by Schultz and Raleigh (1933) in the seedling USDA 41956 with a Chilean variety in its background. CPC 1673, an *S. andigena* clone in the Commonwealth Potato Collection (England) also showed extreme resistance. Another source is the wild species, *S. acaule*.

A single dominant gene, Xi, governs extreme resistance to PVX in *S. acaule* (Cockerham, 1958; Ross, 1961). The alleles Xn and x gave hypersensitive and susceptible reaction, respectively. Xi is dominant over Xn. The genetic relationship between Xi and Xn suggests that extreme resistance (due to Xi) is an extreme form of hypersensitivity.

4.10.3 Potato viruses A (PVA), Y (PVY) and S (PVS)

Resistance to infection by these viruses is known and most likely polygenic in inheritance. Hypersensitivity to PVA, PVY and PVS and immunity to PVA and PVY have also been identified. Fig. 6 shows the typical symptoms caused by PVY.

Single dominant genes Na and Nc condition hypersensitive reaction to PVA and PVY^C, respectively (Cockerham, 1943). Gene Ns, identified from a Bolivian Andigena clone (PI 258907) determines hypersensitivity to PVS (Baerecke, 1967).

The gene Na, conditioning hypersensitivity to all strains of PVA is closely linked to N_x (hypersensitivity to PVX). Most cultivated varieties, e.g. Bintje, Eersteling, Grata, Irish Cobbler, Katahdin, etc., carrying gene N_x are also hypersensitive to PVA (Wiersema, 1972). The close linkage between Na and N_x is very convenient from a breeding standpoint.

The gene Nc which conditions hypersensitivity to PVY^C, an unimportant strain of PVY, does not confer resistance to strains PVY^O and PVY^N. No genes for hypersensitivity to PVY^O and PVY^N strains are available (Wiersema, 1972).

Immunity to PVA and PVY is controlled by a single dominant gene and has been identified in *S. stoloniferum* (Cockerham, 1955; Ross, 1961). Like the immunity to PVX, extreme resistance to PVY is governed by three alleles. The gene for immunity to PVY and PVA only needs to be combined with gene Xi (extreme reaction to PVX) to obtain complete protection against all strains of PVA, PVY, and PVX. Therefore, breeders prefer breeding for immunity to all three viruses to breeding for hypersensity because only two genes are needed to be combined into a new clone.

Fig. 6. Typical symptoms caused by PVY.

5. Varietal Improvement Schemes

Potato breeding follows the same fundamental principle as in other crops—it involves selection of the most desirable genotype for a specific purpose. The raw materials (or variability) for selection could arise from natural or artificially induced variations. Introduction of exotic germplasm and spontaneous mutations (including naturally occuring gross chromosomal changes, e.g. shifts in ploidy level) fall under natural variations.

Sexual hybridization between potato clones is the traditional method of generating artificially induced variations. Induction of mutation, chromosomal aberrations, and shifts in ploidy level also create phenotypic and genotypic changes that breeders could work on although, as already stated, their overall contribution to varietal improvement of potato has been limited. Nevertheless, they are sources of variations that may be utilized whenever desirable variants arise because vegetative propagation insures that such variants remain true-to-type. Genetic changes could also occur in tissue-culture propagation of potato and as such, may add to exploitable variation. A sophisticated approach currently under development is the use of protoplast fusion to generate new variation. Variations among plantlets derived from pure protoplast cultures are also being explored. However, it may take some time before such method can be included among the plant breeder's arsenal of routine breeding techniques if ever the approach proves feasible.

This section is divided into two broad topics. First, emphasis is placed on traditional breeding techniques including introduction, hybridization and selection. Subtopics under each section are provided to elucidate relevant subjects. Second, non-traditional or unconventional breeding methods are presented to provide a broad view of the genetic

improvement efforts in an important food crop like potato. Topics such as breeding possibilities at the dihaploid level, mutation breeding, tissue culture and protoplast fusion techniques, and the development of TPS (true potato seed) technology are included. While it may be argued that most potato breeding is technology rather than science (Howard, 1970), it does not mean that plant breeders can ignore advances in basic scientific knowledge which may be important in facilitating their breeding efforts and/or understanding better the rationale of the approaches they have undertaken.

5.1 Conventional breeding methods

Germplasm introduction, screening of genetic materials for major characters of importance, release and/or utilization of elite clones in a program of hybridization and selection, are collectively still the "bread and butter" of potato breeding programs throughout the world. Although the levels of sophistication and the magnitude of efforts may vary, much of potato breeding is, and will remain for some time to come, crossing two clones which complement each other in terms of important traits in order to select from the offsprings a new clone which combines the good qualities of both parents (Howard, 1978).

Some programs, especially those involved in breeding for special traits like processing quality and resistance to environmental stress such as high temperatures, have utilized population breeding methods because of the relative genetic complexity and/or low gene frequency of desirable alleles of the traits being dealt with. Backcross method has also been widely used in breeding for disease resistance especially when genetic control is fairly simple and the source of resistance is an unadapted clone.

5.1.1 Germplasm introduction

Potato is indigenous to the Andean regions of South America (particularly Peru and Bolivia) and was undoubtedly domesticated there. It is there where the greatest amount of genetic diversity occurs. Many wild species can also be found in Mexico and Central America but these never seem to have been taken into cultivation and the apparently indigenous forms of *S. tuberosum* there all seem to have come from South America, probably in the early post-conquest days (Hawkes, 1978).

The history of potato development as a crop in Europe, North America and the rest of the world traces back to introductions from South America, first into Spain in 1570 and secondly into England a little later. There has been some controversy as to what region of South America the original introductions into Europe came from and whether subspecies *tuberosum* from Chile or subspecies *andigena* from the Andes was first introduced (Juzepczuk and Bukasov, 1929; Salaman, 1964; Salaman and Hawkes, 1949; Salaman, 1954; Hawkes, 1967). Regardless of the disagreements, the movement of potato and its subsequent transformation into a major food crop constitute a classic example of the importance of plant introduction to agricultural development.

Introduction of diverse genetic materials continues to be an important component of varietal development in potato. This must be so especially when the limited genetic variability from which present day Tuberosum cultivars have been bred is considered (Simmonds, 1962). The original introductions from South America were likely few and further decimation of this germplasm by the late blight epidemic of the 1840's must have reduced the store of variability even further. The difficulty of replacing old potato cultivars with new varieties coming from intra-Tuberosum crosses partly attests to the limitations imposed by narrow variability.

Already, there are indications that infusion of diverse materials into the Tuberosum gene pool leads to significant heterosis for yield. Glendinning (1969) found a 13% yield improvement of Andigena x Tuberosum crosses over Tuberosum x Tuberosum crosses, the two progeny groups having similar mean maturities. Other workers (Toxopeus, 1952; Rothacker, 1962; Cubillos and Plaisted, 1976; Tarn and Tai, 1977) provided supporting evidences to underscore the importance of genetic diversity in further improvement of potato. The need to exploit the existing variability has been eloquently described in an assay on this topic by Bennett (1965).

Every breeding outfit must have its own store of variability from which the plant breeder could readily draw materials essential to his program. In countries where potato ranks as a major food crop, the task of collection, maintaining, cataloguing, and distribution of introductions has become a specialized service rendered by a national potato introduction station or agency. Examples of these national collection centers are: USDA potato collection in Sturgeon Bay, Wisconsin; the Dutch potato collection at Wageningen; and the Commonwealth Potato Collection in Scotland. Plant breeders in these countries no longer need to worry about maintaining their own individual collection, although to a limited extent, each breeder invariably keeps a core of elite clones that are considered the mainstay of a specific program. These clones are however usually duplicates of those in the national collection center and are only kept for easier access.

The largest single collection of potato species, cultivated and wild, is held at the International Potato Center (CIP) in Peru. Being at the center of origin and diversity, the CIP collection is considerably augmented year after year. More importantly, valuable genetic materials that would otherwise be irretrievably lost in the aftermath of further agricultural technology and population encroachments into previously undisturbed areas continue to be preserved. CIP scientists have been maintaining, cataloguing and evaluating this collection and distributing important materials therefrom world-wide. The development of tissue-culture technique (Roca et al, 1979) has not only facilitated the transfer of germplasm from CIP but also effectively removed the danger of introducing certain pathogens and pests unknown in countries where potato is not a native crop.

Developing countries, especially in tropical areas where potato is still a minor crop, either do not yet have the capability nor likely the urgent need to maintain collections in the manner and scale that is being done in other countries (or institutions) such as those mentioned above. Much of the effort heretofore had been restricted to variety introductions from temperate countries for testing under local conditions and eventually, release of outstanding clones for commercial production. There is however a growing interest in some of the developing countries to embark on their own breeding program for more extensive crop development (see Section 1). In a few cases, hybridization and selection on a limited scale have been in place for some time now. However, the genetic base in these breeding programs is almost always restricted to introduced Tuberosum cultivars which, as a gene pool by itself, is already narrow. Therefore, the chance of a significantly improved clone arising from such programs is remote even if one considers realistically that the standard of varietal acceptance in these countries is conceivably less rigorous.

Without going to the extent of establishing a germplasm center, it is easily possible for national potato programs to infuse genetic diversity into their breeding activities. A wide range of materials is generally readily available in true seed or clonal forms from large collection centers such as at CIP, USDA, and others. As already mentioned, the transfer of

tissue-cultured materials and other pathogen-tested clones should appreciably ease the fears of introducing, along with the clones, dangerous pests and diseases.

A pervasive willingness to share genetic materials exists among the major germplasm repositories. However, national programs should reciprocally develop an effective system to receive and multiply the introduced materials prior to their evaluation and utilization. Much of the difficulty lies in the transfer of tubers which, being in an active metabolic state, do not last very long in transit. Some national programs often strictly adhere to the principles of plant quarantine even without the basic facilities to keep introductions in viable state and test them accordingly. As a result, tuber introductions are almost always spoiled before they are received by research stations or other requesting agencies.

Plant quarantine is unquestionably essential to prevent the introduction of harmful pests and diseases. Nonetheless, a certain degree of flexibility may be maintained without unduly sacrificing the principles of disease and pest isolation especially where introductions come in tissue-culture form or guaranteed to be pathogen-free. Without this flexibility or better yet, an organized system for receiving and utilizing introductions, much time, money and effort spent by germplasm donors will continue to be unfairly wasted.

5.1.2 Evaluation of introductions

Soon after sufficient quantity of the introduced materials has been multiplied, these are evaluated according to the purpose for which materials were obtained. These tests, or series of tests as the case may be, could involve evaluation for yield and other horticultural characters, resistance to pests and diseases, certain quality attributes, or other traits that particular program considers essential in a specific geographical location.

In almost all cases, successful evaluation generally requires interdisciplinary cooperation between plant breeders, horticulturists, plant pathologists, entomologists, etc. The appropriate combination of discipline obviously depends upon the character under evaluation. Even in certain disciplines, area specialization necessitates a choice of the proper individual to include in a team of cooperators. For example, a fungal pathologist should be the specific person working with breeders in screening for resistance to late blight while a virologist is more appropriate for viral disease. Because of the diversity of disease and pest problems in potato, a team of scientists should ideally encompass most of the major disciplines and their specialized areas.

It has been mentioned that the evaluation of introductions (especially commercial cultivars) in developing countries without any ongoing breeding programs has been limited to determining their potential for commercial production. In most cases, a variety testing program would include evaluation for yield and other important horticultural attributes, relative resistance to diseases, and observations on tuber appearances such as shape, size and flesh color, where these traits contribute to acceptability standards. For example, round oval tuber with yellow flesh is preferred over other types in Indonesia. The series of tests that an introduction ideally should go through is depicted in Fig. 7.

It is important to note that the good state of health of introductions, especially with regards to virus problems, should be maintained during the multiplication process. Otherwise, the evaluation trials particularly relating to general yield performance will be biased against virus-infected clones. Where there is no scheme for insuring healthy and rapid clonal propagation, the least that can be done is to practise positive mass selection of healthy clones to produce reasonably healthy tuber samples for trials.

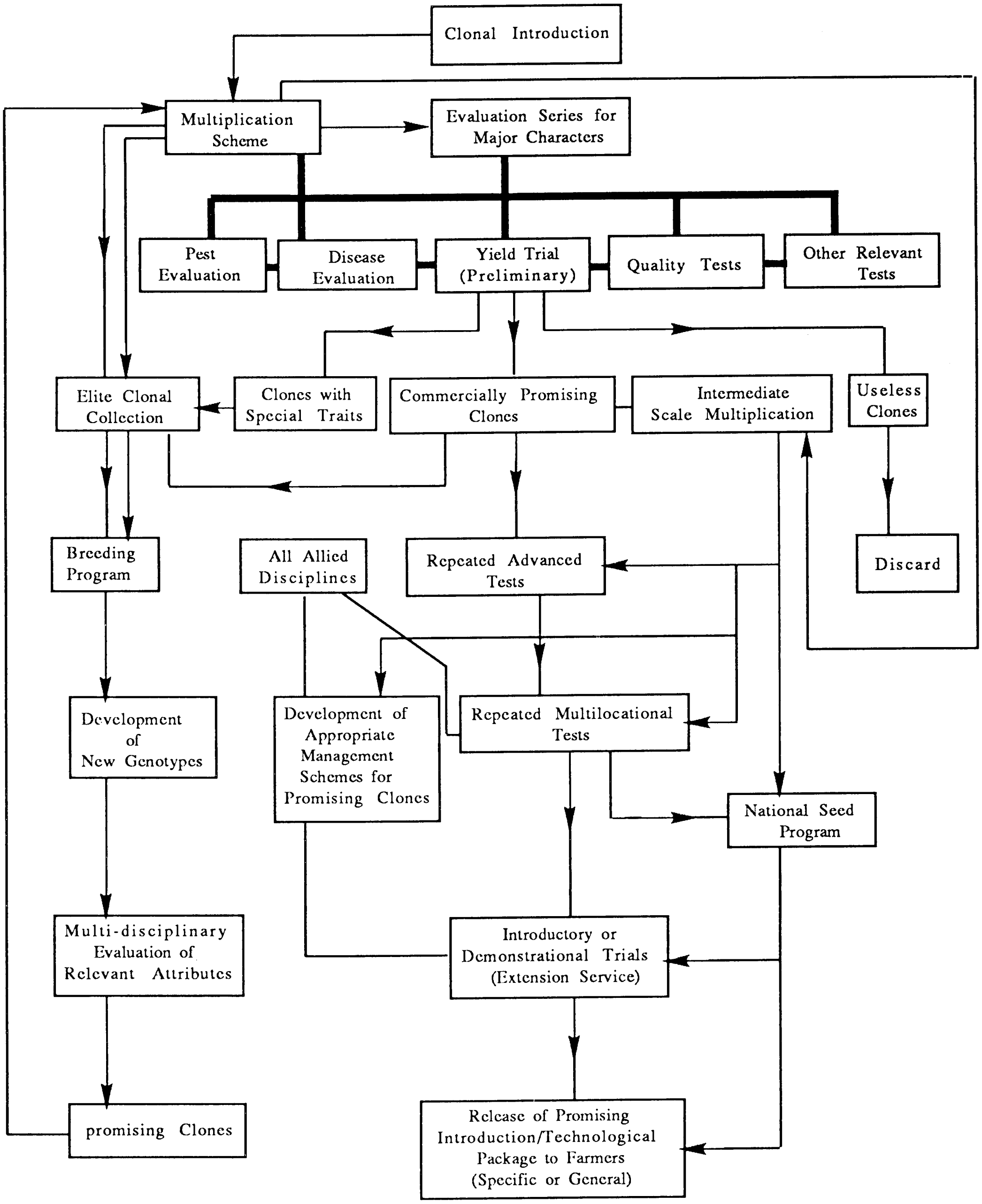

Fig. 7. An idealized flowchart for potato germplasm introduction, evaluation and utilization in a developing country with an on-going breeding program(solid line with arrow at the end = flow of materials; solid line with arrow in the middle = flow of information).

5.1.3 Utilization of introductions

Practically speaking, introductions serve no purpose unless they find their use directly into the agricultural production sector or contribute useful genes they may carry in the development of improved cultivars. In countries without breeding programs and which import only commercial varieties for testing, unadapted clones simply become obscure and eventually lost. Outstanding clones, however, are almost always released as commercial cultivars especially when seed are readily available from exporting nations and further importation is considered economically feasible.

Where a breeding program and a concomitant collection exist, clones that are not outstanding commercially, but carrying special trait(s) such as resistance to important diseases and pests, outstanding quality, etc., should revert back to the germplasm assembly for maintenance and use in breeding activities. It is tempting to imply that ideally all introductions should be maintained by all means but consideration of available resources and technology in developing countries will promptly show that keeping only the elite clones is a far more rational approach than non-selective propagation of all. The latter could be left to large germplasm collection centers, national, regional, or international in scope.

The International Potato Center has, in recent years, developed alternative regional gene banks such as at Colombia and the Philippines. Once fully operational, these regional gene banks could very well serve the needs of national programs within each region and should further justify a program of only selective germplasm maintenance for a specific country.

A diagram of germplasm flow in Fig. 7 illustrates an idealized stepwise movement of clonal introductions from the time they are received until they are utilized. An assumption is made that the introductions are potentially useful commercial cultivars and the scenario is a developing country with an ongoing breeding, elite clonal maintenance and seed production program.

5.1.4. Hybridization and selection

In a catch-all sense, hybridization entails a directed generation of variability for the purpose of choosing (selecting) an improved type. In potato, such variation is immediately released upon crossing a pair of clones because of the inherent heterozygosity of all cultivars. Potato breeding, therefore, appears at first glance to be a simple matter of selecting the most desirable seedlings in the "F_1" generation and asexually mass-propagating the selections thereafter. However, as already described in Section 3, the consequences of vegetative propagation, genetic status, and the tetraploid nature of potato, easily offset the above advantage. Most of the economically important characters in potato are also genetically complex and easily influenced by environmental vagaries that it is virtually impossible to select for them in the early clonal generations.

In this section, the important technical aspects of hybridization are discussed initally. Thereafter, methods of breeding and selection are given. Finally, breeding for specific traits, especially those considered of prime importance in the tropical countries, are provided.

5.1.4.1. Establishment of priorities for breeding

Potato is a prime example of a major food crop with multitude of problems. Depending upon the country, these problems could broadly range from aspects of general performance and adaptation, pests and diseases, and quality attributes for a wide array of usage. Considering that each of these problem categories further subdivides into a number of

specific problems, potato breeders are easily confronted with a host of possible breeding objectives.

Because of this multiplicity of problems, the chance of breeding a successful potato variety is small. Plaisted (1966) estimated that on the average, a breeder can expect to produce a significant variety only once in 15 to 20 years. Wiersema (1961) calculated that only one out of 150,000 seedlings reaches the "List of Varieties" in Holland.

In an overview on this apparent dilemma, Simmonds (1969) very clearly stated that realism is the first important requirement in framing a potato breeding program. Using an example, he arrived at the clearcut conclusion that, breeders must either select for fewer characters or select less intensively.

Comparing the two alternatives, it is far better to review the possible breeding goals under certain conditions and synthesize a set of simplified priorities rather than have a broad range of objectives which is difficult to satisfy *en toto*. Moreover, exercising less stringent selection to encompass multiple objectives effectively reduces to breeding for fewer characters unless a good selection index (Tai, 1977) can be easily found, but even assuming so, it is doubtful whether it can be adopted as a practical breeding tool (Simmonds, 1969).

Establishing a set of simplified breeding objectives may entail a number of coordinated activities. First, a survey of commercially grown varieties should provide the breeders with information as to which are the most popularly grown cultivars, their assets and liabilities. Where a well-organized extension service exists, their assistance in identifying the most pressing production problems should be availed of. Oftentimes, experimentation may be necessary to decide which problems are the most critical. For example, studies on extent of yield reduction, intensity of distribution, etc. may help in prioritizing the diseases and/or pests problems to solve through breeding. Plant breeders and cooperating scientists should neither neglect the importance of contact with farmers and observations of their commercial fields for aid in decision-making. Before formulating a breeding program, all possible sources of information should be examined to insure that priorities are clearcut and relevant.

In developing countries, potato breeders can seek comfort in the fact that the requirements for any new variety are less rigid than where potato is commercially a highly developed crop. The limited and unsophisticated utilization of potato in developing countries practically minimizes breeding for high quality both for processing and immediate consumption. Statistics on potato utilization in developing countries show that processing is not an important component (Horton, 1978). However, times do change and breeders should always be prepared to respond to contemporary market demands. At the present time, it may be safely presumed that potato breeders in developing countries should concern themselves mostly with breeding for high yield and adaptability (especially to short daylength and relatively high temperatures), resistance to major pests and diseases, and perhaps, to some extent, a few important quality attributes. Some countries have preferences for example for particular tuber shapes, flesh and skin colors, and size. Most of these traits are, however, easier to breed for than cooking and processing quality components in view of their relatively simple genetic control (see Section 4).

With respect to disease and pest resistance as breeding objectives, a certain amount of realism will again be needed. A survey of production areas will invariably reveal a variety of pests and diseases but not all likely deserve the breeder's attention. In some cases, chemical control of certain diseases or pests or some other means of control may prove to be highly economical already. A good seeed program can practically eliminate the need to breed for virus resistance, and incorporation of stem-cutting techniques in the scheme is effective in controlling blackleg (*Erwinia carotovora* var *atroseptica*) and possibly other tuber-borne diseases (Hardie, 1971 ; Calvert, 1973). Naturally, it can be strongly argued with good reason that the use of resistant varieties is still the cheapest method of controlling pests and diseases. However, a successful plant breeder is always a practical one and considering the many problems he has to solve, one less objective contributes to his chances everytime.

5.1.4.2. Choice of parental breeding stocks

The survey of locally grown cultivars can provide breeders with good benchmark information to help him identify potential parent clones for the breeding program. Oftentimes, a situation exists where some cultivars are deficient only in a few important attributes to become a highly successful variety. If these are available, the problem becomes one of finding among other clones those traits which adequately complement the outstanding characteristics of the other parents. If not available, efforts should be made to secure the valuable germplasm from other sources.

Sometimes, the desired combination of characters may already be in an established cultivar elsewhere and initiating a breeding program may, in the long run, be more costly than importing that cultivar. The value of germplasm introduction on this regard is very obvious. The testing program for introduced varieties should not lose sight of the general breeding goals to insure that potential solutions are properly adopted.

In general, four groups of parents are available to potato breeders. These are varieties of Group Tuberosum, Group Andigena, cultivated diploids, and wild species. Tuberosum cultivars are adapted to long days typical of summers in temperate countries. Under the short days of the tropics, these cultivars tend to mature earlier and therefore, are comparatively less productive. Nevertheless, most of the potato varieties grown in the tropical countries (except in South America where potato is indigenous) belong to Group Tuberosum.

When the characters of interest to potato breeders are not available in the Tuberosum gene pool, the next best source is Group Andigena. There is undoubtedly a substantial amount of variability present in the Andigena gene pool (Plaisted, 1977). Valuable genes for potato breeding that are known to be present in Group Andigena are: field resistance to late blight ; immunity to PVY and PVX; resistance to PVS, common scab, wart and Verticillium wilt; and resistance to aphid species *Myzus persicae* and *Macrosiphum euphorbiae* (see Table 1). The gene pool itself had incontrovertibly given rise to the present day Tuberosum gene pool when small samples of short-day adapted Andigena potatoes introduced into Europe were subsequently selected for long day adaptation there. Simmonds (1966) and Plaisted (1972) have attempted to repeat what undoubtedly was a slow adaptation process by practising intense selection for key Tuberosum characters on genetically broad Andigena populations. All indications are that the morpho-physiological changes which characterized the evolution of Tuberosum from Andigena gene pool are indeed repeatable.

The cultivated diploids are likewise a highly variable group with a tremendous reserve of genetic potential which has remain largely untapped. Useful genes in this group range from : resistance to virus diseases such as PVA, PVX, PVY and leafroll; resistance to late

blight, ring rot, bacterial wilt and Verticillium wilt; resistance to insects such as flea beetle and aphids; nematode resistance; frost resistance; and high dry matter content (see Table 1). There appears to be no difficulty in crossing cultivated diploids and tetraploids. Marks (1966) observed that the results of such crosses are often tetraploid, not the expected triploid offspring, primarily due to the appreciable frequency and normal functioning of unreduced gametes in the diploid parent.

A gene pool of last resort is the wild species. Potato breeders have used wild species in hybridization programs only when the genes sought after are not available in cultivated groups or even if so, intensity or level of gene effects such as those conditioning resistance to diseases or pests is low. The conservatism in the use of wild species for breeding purposes is understandable when one considers the length of time it takes to transfer the useful genes into the genetic background of cultivated potato. Undesirable characters from the wild often accompany such transfer and occasionally, these traits are difficult to eliminate especially if they are closely linked to the gene(s) of interest to the breeder. A prime example of valuable genes successfully transferred from the wild species into *S. tuberosum* are the R-genes for resistance to late blight from *S. demissum*. Other potentially useful genes from wild species are : resistance to golden nematode in *S. vernii, S. oplocense, S. spegazinii, S. sparsipilum, S. boliviense, S. brevicaule,* and *S. megistacrolobum* (Ellenby, 1952; Ross and Huijsman, 1969; Deshmukh and Weischer, 1970); resistance to aphids in *S. polyadenium*, *S. tarijense, S. berthaultii*, and other wild species (Gibson, 1971; Radcliffe and Lauer, 1971); resistance to Colorado beetle in *S. chacoense*; extreme resistance to all strains of PVY in *S. stoloniferum* (Cockerham, 1970); resistance to PLRV in *S. demissum, S. acaule, S. chacoense* and *S. stoloniferum* (Wiersema, 1972); and many more (see Table 1).

As cited in Section 2, most wild and cultivated diploid potato species can cross easily and the resulting F_1's are fertile and vigorous. The absence of strong breeding barriers between most potato species is a tremendous advantage to plant breeders because it considerably widens the range of genetic variabliity that they can utilize.

5.1.4.3. Breeding methods

Traditionally, the systems of breeding used in potato have been by pedigree method or in some cases, by backcross method. Population breeding methods, such as recurrent selection, have gained acceptance among breeders involved in improving clones for characters conditioned by polygenes, e.g., yield, dry matter content, and other important traits, especially those contributing to processing qualities (plaisted, 1966).

5.1.4.3.1. Pedigree breeding

As already mentioned, much of potato breeding has been and will perhaps remain for some time, crossing a pair of clones which complement each other in desirable attributes in order to select a new clone possessing the good qualities of both parents. In general, a series of crosses is usually necessary to accumulate a number of good traits into a single clone. This is the so-called pedigree breeding method.

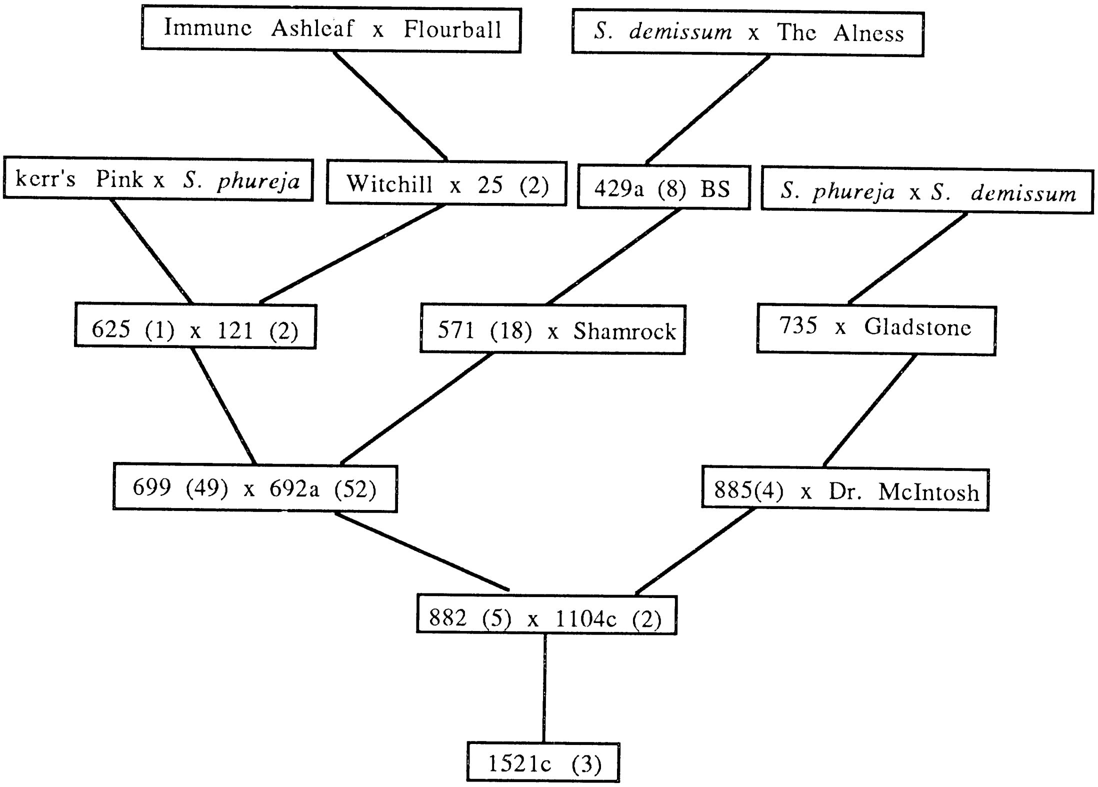

Fig. 8. Pedigree of Roslin Ebrur (after Black, 1972).

Pedigree method works very well when the characters to be accumulated in a new clone are simply inherited and conditioned by dominant genes. This is expected since the desirable genotypes appear in high frequencies and can be selected right away among the immediate hybrid progenies. Assuming that only two dominant genes are to be combined and chromosome segregation is random, the proportion of desirable genotypes can range from 25—100% depending upon the genetic configuration of the parental clones (Table 5). The least proportion (25%) arises only from simplex x simplex mating but even that frequency is already sufficiently large considering that thousands of progenies, not hundreds, are normally handled in a potato breeding program. A good example of variety produced by pedigree method is Roslin Eburu, a variety released in Kenya which occupies most of the acreage in East Africa (Black, 1972). Although its field resistance to blight is only moderate, the degree of resistance it possesses together with its adaptation to short-day conditions and its cropping propensity has established it over a wide area. The pedigree record of Roslin Eburu is shown in Fig. 8. Note the series of crosses made before arriving at the final clone.

With traits that are controlled largely by recessive genes, the proportion of desirable genotypes among hybrid progenies is drastically reduced and can only be recovered (assuming only random chromosome segregation) when both parents are at least duplex for all the genetic factors in question. Even so, the expected number of progenies homozygous for the recessive alleles (assuming that only two genes are to be combined) is only one in

1,296 seedlings. This proportion is greatly incremented as the dosage of the recessive alleles increase in each parent. For example, using the two - gene model again, this proportion is now 1/8 if one of the parent clones is already homozygous recessive (nulliplex relative to the dominant gene) for one of two genes and has the other in triple dose (simplex for the dominant gene) while the other parent has both recessive genes in triple dose, i.e., the genetic cross configuration is Aaaabbbb x AaaaBbbb.

Simplified genetic situations as the above naturally are rarely, if ever, encountered in actual potato breeding partly because breeders are normally concerned with combining more than two characters into a single clone, even in an idealized case where the major traits sought after are simply inherited. Moreover, random chromatid segregation is also known to exist in *S. tubersosum*. This phenomenon will only slightly alter the genetic ratios but it will enable triplex parents (AAAa) to produce a low frequency of nulliplex (aa) gametes or conversely, simplex parents (Aaaa) to produce duplex gametes (AA). Catcheside (1959) also pointed out that production and functioning of aneuploid gametes could give results similar to those expected from chromatid segregation. This appears to have some cytological basis as normal meiosis in *S. tuberosum* usually shows, in addition to quadrivalents and bivalents, also univalents and trivalents (Wangenheim, 1955; Swaminathan, 1954a; 1954b). Univalents and trivalents could lead to the formation of aneuploid gametes.

Table 5. Theoretical frequency of desirable genotypes, i.e. progenies which combine the dominant genes from complementary parents, in the immediate hybrid population in all possible mating schemes[a].

Type of of mating	Hypothetical parent genotype	Expected frequency of desired genotypes (%)
simplex x simplex	Aaaabbbb x aaaaBbbb	25
duplex x duplex	AAaabbbb x aaaaBBbb	70
triplex x triplex	AAAabbbb x aaaaBBBb	100
quadruplex x quadruplex	AAAAbbbb x aaaaBBBB	100
simplex x duplex	Aaaabbbb x aaaaBBbb	42
simplex x triplex	Aaaabbbb x aaaaBBBb	50
simplex x quadruplex	Aaaabbbb x aaaaBBBB	50
duplex x triplex	AAaabbbb x aaaaBBBb	83
duplex x quadruplex	AAaabbbb x aaaaBBBB	83
triplex x quadruplex	AAAabbbb x aaaaBBBB	100

[a]Using a two-gene model and assuming random chromosome segregation.

5.1.4.3.2. Backcross breeding

When one of the parent clones in a cross is commercially an unadapted type but carries an important trait lacking in the other parent (usually a valuable commercial variety), breeders resort to the system of backcrossing. A good example is the transfer of resistance to golden nematode (*Globodera rostochiensis*) from Group Andigena to *S. tuberosum* cultivars adapted to the northern belt of the United States (Plaisted, 1966). Another is the incorporation of major R - gene resistance to late blight from the wild hexaploid species, *S. demissum*, to tetraploid *S. tuberosum* (Marks, 1960).

As in other crop plants, the backcross method in potato is greatly facilitated if the character under transfer is simply inherited and conditioned by a dominant gene. In the simplest case of incorporating a monogenic dominant gene, segregation occurs in the immediate F_1 if the donor parent is simplex (Aaaa) or duplex (AAaa). Naturally, the recurrent parent (or the recipient) is nulliplex (aaaa) for the gene. The proportions of hybrid progenies with the desired dominant gene are 50% and 83%, for simplex and duplex donors, respectively. Thus immediate backcrossing to the recurrent parent is possible assuming that a good selection regime (especially when dealing with pest or disease resistance) is available to pick out the progenies carrying the dominant gene. With triplex (AAAa) or quadruplex (AAAA) donors, there is no observable segregation in the F_1 and backcrossing can proceed more normally. Regardless of the genetic status of the donor, however, every backcross generation thereafter will exhibit segregation for the dominant gene under transfer. Therefore, the appropriate backcross derivatives to use in further backcrossing must be continually selected.

The backcross procedure is far more complicated and slower when the desirable gene from the donor parent is inherited in a recessive fashion. In the single gene model where the recurrent parent does not carry the recessive allele, i.e., AAAA, the dominant allele masks the desirable recessive allele in every generation. Thus, it is necessary for the breeder either to self or intercross progenies every time in order to select the clone which expresses the desired trait for use in further backcrosses. Alternatively, the breeder can dispense with progeny tests and continuously backcross using a representative sample of progenies in every backcross. Bulk-pollen hybridization can facilitate this procedure. However, though faster and possibly less time consuming, there is always the danger that the gene under transfer could be inadvertently lost in the process. This problem could become magnified especially when progenies have a wide range of flowering time that some unavoidably cannot contribute to the next generation. A possible solution might be to regularly intersperse the progeny test every 2 or 3 backcrosses as a spot check for the presence or absence of the desired gene.

A situation may be visualized whereby the intended recurrent parent is already heterozygous for the desired recessive gene. In such special case, the pedigree method is more suitable than the time-consuming, tedious backcross system assuming that another heterozygous parent is available so as to uncover the homozygous recessives either in the immediate hybrid progenies or from F_1 intercrosses, as the case may be. Selfing heterozygous clones (especially those with two or three doses of the recessive allele) should, of course, reveal the homozygous recessives immediately. However, potato is an outbreeder and is known to exhibit inbreeding depression upon selfing (Krantz, 1946). Nevertheless, such homozygous recessives from a selfing program may be used directly as parents.

The cultivated potato is highly heterozygous and therefore, the genetic background of the recurrent clone is virtually impossible to recover. Nonetheless, further selection among the F_1's and backcross derivatives carrying the desired gene under transfer, for general traits more or less typical or progressively near the recurrent parent, should accelerate the reconstitution of a desirable genetic milieu. This is especially useful when the donor parent is a highly unadapted type, e.g. wild species. Selection of such derivatives is considered equivalent to saving one or two backcrosses (Briggs and Knowles, 1967).

The number of backcrosses to make depends upon a particular situation. Generally, it can range from three to ten. As already noted, the potato breeder cannot fully reconstitute the exact genetic background of the recipient clone. Therefore, as soon as the frequency of commercially adapted types carrying the desired gene(s) being transferred is already

significant in a specific backcross generation, the derivatives are often subsequently handled by pedigree method to select the best clones. Obviously, the number of backcrosses required to reach such a stage is dependent upon the nature of the donor parent—wild species as gene donors will require more, for example, than say donors from Group Andigena, when backcrossed to *S. tuberosum* cultivars.

Progeny testing of derivatives from the last intended backcross generation cannot be dispensed with when the gene under transfer is recessive. Pedigree handling of the homozygous recessives follows thereafter. With a dominant gene, this procedure is not necessary as long as the last backcross derivatives are effectively selected.

5.1.4.3.3. Population breeding

Many economically important characters in crop plants exhibit polygenic inheritance. In contrast with the classical Mendelian genes, i.e., those with large, easily discernible effects, polygenes do not follow clearcut segregation ratios and generally, there is no one to one correspondence between the phenotype and the genotype of an individual. The reasons for these peculiarities are as follows: many genes each with small individual effects control polygenic characters; gene interactions are more often a rule than an exception; and the genotypic expression is highly influenced by environment.

In potato, there too are many important characters under polygenic control, e.g., yield, maturity (under a specific daylength), dry matter, and certainly, most processing quality attributes such as after-cooking darkening, levels of reducing sugars, etc. In breeding for these traits, breeders are often faced with the problem of how to carry out selection in a most effective and efficient manner.

The cultivated potato is a tetraploid which means that a gene is present four times in an individual. Using for simplicity just a two-gene model in which we assume that there only two alleles per locus, that each gene contributes equally to the phenotype, and that dominance, epistasis, and environmental effects are completely absent, only two genotypes (which may be symbolically represented as AAAABBBB and aaaabbbb) in a hybrid population exactly match their phenotypic expressions. Other phenotypic values are already, even in such exceedingly simple model, represented by a range of two to five genotypes. Selection of a particular phenotype therefore will not necessarily indicate its true genotype.

In real situations, the simplifying assumptions of the above model certainly do not hold. Breeders usually can anticipate a preponderance of loci conditioning complex charactes, interaction between loci, unequal contribution of loci to the total phenotype, significant environmental effects and varying dominance levels at different loci. It is thus easy to visualize how the idiosyncracies of polygenes can greatly confound the breeder's dilemma.

Recurrent selection as a population breeding method has received increasing use for improving characters in potato that are under polygenic control (Houghland *et al,* 1961; Plaisted and Peterson, 1963; Stevenson et al, 1954; Mendoza, 1976; Opeña, 1976; Tarn *et al,* 1977). The method is designed to increase the frequency of superior genotypes in breeding stocks. Recurrent selection accomplishes this by increasing the frequency of superior genes in the gene pool and by increasing the chances or genetic recombination to occur.

As the name implies, recurrent selection systems are cyclic in nature. Hull (1952) succinctly defined the method: "Recurrent selection was meant to include reselection generation after generation, with interbreeding of selects to provide for genetic recombination. Thus, selection among isolates, inbred lines, or clones is not recurrent until selects are interbred and a new cycle of selection is initiated". Each cycle requires evaluation

and maintenance of selections, and intercrossing the superior selection (or their self progenies) in all possible combinations and bulking of equal amount of seeds from each cross to initiate the next cycle.

The evaluation of selections in each cycle may be based simply on their phenotypic expressions for character of interest or on progeny test. The first method is called phenotypic recurrent selection. As the value of a selection is assessed from information from a single individual, the method is expected to work well for characters with relatively high heritability. Plaisted and Peterson (1963) reported nonetheless the efficacy of phentypic recurrent selection in improving potato dry matter content, a genetically complex trait. Three cycles of recurrent selection increased the dry matter 20% above that of cv. Katahdin and 2 cycles increased it 8% above the average of Delus, Green Mountain, Saco, Houma and Merrimack, cultivars which were chosen as parental clones because of their high specific gravity. Although their method falls under phenotypic recurrent selection, it must be pointed out, however, that their selection of clones for each intercrossing cycle was based on three-year tests. Here again, vegetative propagation enables multiplication of selections without loss of genetic identity and clearly provides potato breeders with a unique advantage not normally available to seed crop breeders.

As an accessory tool in recurrent selection, progeny tests aid breeders in assessing the genetic worth of selection as parent stocks. Genetically variable testers give rise to recurrent selection for general combining ability. When the tester is genetically narrow, recurrent selection is for specific combining ability.

The average performance of a potato clone as a parent in a range of crosses is referred to as the general combining ability of that clone. This information is particularly valuable in the sense that it measures the breeding value or the ability of a clone to pass on its good characteristics to its offsprings. Some clones may, by themselves, be outstanding but be poor parental stocks. Some studies have clearly shown the existence of differences in combining ability among clones for yield, specific gravity, and tuber appearance (Sanford, 1961; Plaisted *et al,* 1962). Plaisted (1966) cited how progeny tests have been used to identify clones which on the average produced progenies less apt to turn dark after cooking than most other clones.

Using mainly good combining clones in the hybridization program should considerably help breeders to further refine the breeding activities. Progeny tests, in other words, provide breeders with a rational method of choosing parents.

5.1.4.4 Flowering induction and enhancing success of pollinations

The development of flowers and fruits (technically called "berries") in potato is related to source-sink balance in the plant. Without the essential nourishment, flower buds abort or even if full grown flowers have been produced and pollinated by a known pollen-fertile clone, flowers tend to drop. In some cases, berries successfully set but are not retained and tend to abscise before full maturation.

Most cultivated diploid potatoes and wild species are free-flowering types. However, many varieties in the cultivated tetraploids, among which conventional breeding activities are largely confined, produce only a few flowers. In several important varieties such as Bintje and King Edward, flowers are not normally found (Howard, 1970). This can be a serious drawback in breeding and/or genetical studies in that certain desirable crosses may not be possible to make

Two useful methods have been developed to prevent flower bud abscision and enhance its development. Carson and Howard (1954) successfully produced flowers in many varieties, including King Edward, by grafting potato scions on tomato stocks. Thijn (1954) developed the "brick growing" method to induce flowering. Briefly, the method involves growing the sprouted tuber on a brick or tile above soil level and covering it with sand. After the roots have grown into the soil, the sand is washed away thereby exposing the tuber-forming stolons which can then be cut before tubers fully develop.

Both aforementioned methods were designed to eliminate the sink (tubers) for carbohydrates and other assimilates produced by the haulm so that more nourishment is available for flower bud development. Howard (1970) further suggested the removal of axillary buds below the inflorescences for cv. King Edward and some other varieties because their development into shoots tend to compete with the inflorescences for nutrients. With certain potato varieties grafted on to tomato, aerial tubers sometimes profusely develop on or around the region of graft union (personal observation). When such sinks are produced, they should be promptly removed.

Fig. 9. A potato plant growing on brick to induce flowering. Note the exposed roots and mother tuber. Stolons at the base of the stems have already been cut to prevent tuberization.

Other treatments found conducive to flowering in potato are : long days (Patterson, 1953; Steineck, 1957), late planting (Rothacker, 1957) and gibberellic acid application.

Combination of treatments such as growing on bricks, long days and GA application may be necessary for certain clones that produce very sparse flowers (Anon, 1976a). The influence of moderately cool temperatures in enhancement of flowering should not be neglected either. The optimum mean temperature range for flowering in potato is about 16° - 18°C.

The full development of flowers among potato breeding stocks is no guarantee that all planned crosses can be achieved because many Tuberosum varieties are pollen-sterile. Fortunately, most pollen-sterile cultivars have good ovule fertility—ovule sterility appears to be rare. Pollen-sterile varieties can still be used therefore as females in the crossing block. Pollen sterility in potato is under genetic control and has been suggested to be due to a single dominant gene, or to recessive genes, or to gene-cytoplasm interactions (Okuno, 1952: Lamm, 1953; Ross, Peloquin and Hougas, 1964), the causes not mutually exclusive (Grun, Aubertin and Radlow, 1962; Grun and Aubertin, 1965).

Even if known ovule-fertile variety is pollinated by fertile pollen, there is still a tendency among some clones for flowers to abscise and thus, not produce berries. Peloquin and Hougas (1959) found that cutting the stems with flowers from field-grown plants and placing them in jars of water, sometimes containing an antibiotic for bacterial control, can be very successful. Use of nutrient solution does not appear to be necessary. The method allows controlled pollination to be done in the greenhouse where fertilization and subsequent development of berries are less prone to vicissitudes of environment. Wiersema (1950) recommended spraying the inflorescence with 2,4-D or other auxin analogues 2 - 3 days after pollination to minimize flower abscission and enable the ovaries to develop into seeded berries.

5.1.4.5 Other useful considerations

When clones are to be used frequently in crosses or in successive stages such as in a backcross program, it may be worthwhile to collect sufficient quantity of their pollen and preserve their viability for as long as possible. This technique will obviate the need of having parent clones flowering synchronously. Drying the anthers and then storing them at -20°C can preserve pollen viability for as long as two years (King, 1955; Howard, 1958). If subzero storage facilities are not available, storing pollen even at +2.5°C is sufficient to keep pollen alive for about a month (Blomquist and Lauer, 1962).

Storage of true potato seeds poses no difficult problem to breeders. Most potato seed samples, stored dry under normal laboratory conditions, can retain their viability for at least 10 years (Howard, 1978). Cold temperature (-20°C) storage can result in seeds remaining viable for at least 20 years (Howard, 1969; 1975).

As with tubers, true potato seeds exhibit dormancy. However, this resting period disappears after a few weeks in storage (Simmonds, 1963). Soaking dormant seeds in 2,500 ppm gibberellic acid for 48 hours, followed by drying, is effective in breaking true seed dormancy. However, germination is usually not nearly as uniform as seeds in which dormancy was naturally broken in prolonged storage. Howard (1978) observed that Tuberosum seeds stored for 9 months still retain a certain amount of dormancy and seeds stored for 21 or so months often germinate much better than seeds stored for only 9 months.

5.1.4.6 Systems of handling and selection of hybrid progenies

The ultimate goal of potato breeders is to identify and select the clones with the best promise of becoming exceptional cultivars. The variability upon which such selection is

applied becomes available either shortly after hybridization between parental clones, as in the case of pedigree breeding, or developed sequentially as in backcross and recurrent selection methods. As already noted, the penultimate derivatives from the latter breeding schemes are also handled via the same system as the pedigree method.

One of the fundamental prerequisities of successful plant breeding, regardless of which method is used, is the ability to recognize superior types from a limited or vast array of variability. It is here where the skill and keeness of the breeder's perceptive ability are put to a rigid test and where possibly, plant breeding as an art versus science is more than ever discretely manifested. Perhaps, it can also be said that it is here where plant breeding either makes or breaks. Afer all, potential variability left untouched is practically useless.

This section aims to present the activities in potato breeding from the time hybrid seeds are sown until a new variety is released.

5.1.4.6.1 Management of seedling and various clonal generations

Every potato seedling arising from botanical seed is practically virus-free because viruses, excepting spindle tuber viroid (Diener, 1971) are non-transmissible through seeds. As emphasized in Section 3, it is the breeder's task to preserve the selected clones in a virus-free state throughout the various stages of selection and multiplication. In order to insure that they remain so, certain techniques and precautions are considered standard measures in potato breeding.

Growing the seedling generation in an aphid-proof glasshouse or screenhouse is now a common practise where an effectively isolated, clean field to grow them cannot be found. Fig. 10 shows hybrid seedlings in 10cm diameter pots growing alongside virus-indexed clones inside a screenhouse. Combined with regular pest control measures to kill viruliferous aphids, effective soil sterilization, minimal handling of seedlings and proper sanitation including disinfection of hands, tools and other screenhouse equipment, seedlings can often be kept virus-free.

With freshly harvested seeds, dormancy should be broken by gibberellic acid treatment (see Section 5.1.4.5). However, germination is often not as uniform as those seeds whose dormancy had ceased after prolonged storage. The seeds may be sown on pans or other suitable containers, e.g. wooden flats, clay pots, etc., containing appropriate germinating medium. The medium could be sterilized ordinary greenhouse soil mix or if readily available, special sterile medium sold commercially, such as jiffy-mix. These special media, however, often need supplementary nourishment using Hoagland's or other nutrient solutions. When seedlings are large enough, they can be pricked into small plastic or clay pots where they are grown to full maturity.

When only a small amount of seeds are available and a maximum recovery of as many seedlings as possible is desired, seeds may be sown in Petri plates with moist blotting paper. As soon as seedlings have grown to a suitable size, they may also be pricked directly into pots. The size of pots may vary but 10 cm diameter pots are widely used. Pots that are too large permit production of larger tuber sets but effectively reduce the number of seedlings that can be grown per unit area. Smaller pots, on the other hand, will maximize the number of seedlings but tuber sets will be small.

Fig. 10. Hybrid seedlings (left) growing inside an aphid-proof screenhouse to keep them from being infected with viruses. A plastic strip below the pots prevent direct root-soil contact.

Care should be taken that non-random pricking of larger, rapidly germinating seedling is avoided. True seed dormancy and tuber dormancy appear to be correlated and could possibly even share a common biochemical pathway (Simmonds, 1964) and pricking out the rapidly germinating seedlings (short dormancy types) at the expense of late seedlings (long dormancy types) may result in unconscious selection for short tuber dormancy. Such problem could be acute especially when freshly harvested true seeds are sown without prolonged storage. In areas where short dormancy is desirable, the practise may be carried out or even further developed as a selection criterion.

The first clonal generation until the one prior to conducting small scale yield trials should be grown for further selection and multiplication in good seed districts to minimize the chance of viral infection. These areas are usually chosen for being spatially isolated from commercial production zones and/or where aphid populations are significantly low to enable the production of clean, healthy tuber seeds. Rigid pest control measures should also be practised to enhance the success of keeping the clones reasonably healthy.

The preliminary and subsequent yield trials naturally are conducted in commercial production districts and are aimed to compare the performance of selected clones against the leading cultivars. At these testing stages, the chance that clones will become infected is high and plans are usually made to insure an adequate supply of clean seeds for the various trials. A good scheme to multiply promising clones, once they are entered in variety trials or even a year or so earlier, should be an essential corollary activity that is closely tied up with the breeding program. Without such system, there is always the danger that promising clones may be selected against in the variety testing program due to virus infection. Breeders could greatly assist in the scheme by carrying out apparently healthy single plant selections from

promising clones and planting them out in individual rows to check their health. Infected progeny rows are then immediately destroyed and clean seed stocks are established only from healthy rows. These clean stocks can serve as buffer supply for further multiplication in case the clones unfortunately become infected during the various testing stages.

5.1.4.6.2 Methods of selecting superior clones

Potato breeders often must still deal with a number of important traits even though refinement of objectives had already been established. The necessity to have this multiplicity of selection targets is in large part enforced by the wide and sophisticated variety of usage that potato has come to nowadays. Even if a breeder delimits his goal to a specific type, the multitude of important disease and pest problems confronting potato producers hardly minimize the formidability of potential breeding objectives.

The objective traits naturally will vary in genetic complexity, some highly heritable and relatively easy to breed for, while others are complex and difficult. It is therefore only logical that proper selection pressures be applied at the appropriate stages of variety development. For example, it is ineffective to select for high yields or other complex traits at the seedling stage and in the first few clonal generations. Engel (1957) pointed out the large errors obtained when yields are estimated from observations on single plants or small clonal plots. Moreover, differences in the size of tuber set such as commonly manifested in the first clonal generation confound any possible selection even for relatively less complex traits.

Discarding seedlings that are too weak or too "wild" (types with long stolons and requiring short days for tuberization) may be 100% efficient according to Howard (1978). Contrary to Engel's (1957) findings, Verma (1972) concluded that it is safe to discard low yielding seedlings at the seedling stage itself. These low yielding seedlings are likely those which are weak, however. Maris (1962) and Howard (1963) both agreed that selection at the seedling stage should not be too stringent.

In the first clonal year, selection for such characters as tuber shape and depth of eyes may be efficient enough (Howard,1978). Heavy selection pressure in the first clonal generation, sometimes as high as 90% of the population, was questioned by Tai (1974) since plants in this generation are usually managed in an unconventional scheme (e.g. wide spacing vs. commercial practise). Using quantitative genetic analysis of data from two clonal generations (1st and 2nd), it was concluded that selection for quantitative traits in most cases is less efficient in the first clonal generation than direct selection in the second clonal generation. This corroborates more or less the conclusion of Engel (1957).

The Cornell program of selection among clones (Plaisted, 1966) will perhaps provide a sufficient example of how potato breeders manage the breeding materials when multiple objectives need to be attained. The program is multi-stage with three overlapping phases. In phase one, selection is emphasized for highly repeatable traits such as external appearance (e.g. tuber conformation, flesh/skin color, etc.) and resistance to golden nematode, a major problem in New York. Selection against highly undesirable traits such as after-cooking darkening is also practised even though they recur infrequently. In the second phase, selection for yielding ability of clones is undertaken, mostly based on the comparison of selections against one another but later on, towards the end of the phase, also against a standard check, cv. Katahdin, the principal variety in New York that is less prone to interactions with locations and season than other varieties. Finally, surviving selections are evaluated in the area where they are best adapted to and for the specific purpose for which they were developed. Table 6 provides further details of the Cornell program of selection

among clones generated from hybrid seedlings grown in 3 - inch pots in an aphid-proof glasshouse.

As may be noted, a range of only 0 - 2 clones is projected to remain and possibly be released as new varieties out of the original 30,000 seedlings (Table 6). Indeed, the probability of breeding a useful variety of potato is rather small (see Section 5.1.4.1.1). Hence, large number of seedlings must be raised and a quick, efficient selection scheme to choose the few superior types should be instituted. Raising large numbers of seedlings and producing large numbers of seeds from hybridization are easy enough to do. It is in the selection of seedlings and in the first few clonal generation when they are grown in small clonal plots that the most difficult practical problems in potato breeding are encountered (Howard, 1972).

An essential feature of the system that comes to light is the progressive emphasis and development in selection for yielding ability. From a cursory evaluation at a single location during the third year, the trial is expanded appreciably until in the 7th year and on, it covers six or more locations. It is very important that potato breeders conduct the trial over a number of seasons and locations because there are many economical traits, e.g. yield (Plaisted, 1960; Plaisted and Peterson,1959) , specific gravity (Haddock and Blood, 1939; Plaisted, 1957; and Stevenson *et al,* 1963; Thran, 1958), after-cooking darkening (Dalianis *et al,* 1966), flake quality (Isleib, 1962) and many others, which exhibit variety x season, variety x location, and variety x season x location interactions. Such interactions indicate that there is no predictable trend in the performance of clones over seasons and locations. Some varieties may do well at some locations and/or during certain season but not in others.

Without a certain amount of predictability, the choice of varieties, be they from hybridization or introduction, for recommendation becomes a complicated task. Breeders may surmount the limitations to selection imposed by genotype-environment interaction by restricting recommendations to a particular geographical location. Oftentimes, however, the bases for such recommendations are generally inconsistent. Moreover, it is not all that easy to clearly demarcate geographical areas. The breeder's alternative is to search for a variety which performs consistently over a range of locations and seasons (Akeley, 1958; Plaisted and Peterson, 1959; Plaisted, 1960; Harris, 1974; Tai, 1979). Stability of performance is a valuable attribute and, whenever possible, should be sought after. A cultivar which is widely distributed on account of its consistent performance certainly has demerits in regard to the dynamics of disease or pest epidemic but it greatly simplifies the variety situation, seed production and distribution problems, pest and disease management techniques, agronomic practices, and other important facets of commercial production.

In variety testing, it may be added that techniques could vary to a certain extent between country programs or even between regions within a country, viz. plot dimension, spacing, fertilization rate, cultural and management method, etc. Most, if not all, of these differences are partly dictated by the resource capabilities, needs, or even physical attributes of a particular geographical location. While these differences are inevitable, the multilocational tests within any program should follow uniform practices so that the trial results are comparable across locations and seasons. One might argue that differences artificially imposed during such trials would allow viewing the response of cultivars over a wider range of environmental diversity. On the other hand, the environmental factors even within a restricted locality are no doubt already broad and complex that any controllable variation taken out of any experiment helps in minimizing the complexity of results and facilitating their interpretations.

Other selection methods have been described by different workers (Black, 1953; Howard, 1978). Akeley (1966) described a practical breeding procedure for the development of potato varieties and seedlings with multiple resistance to a range of tuber disorders. While the described methods may vary to a certain degree, the underlying principles of selection in all cases remain the same.

5.1.4.7. Breeding for specific traits

As alluded to in Section 5.1.4.1., potato breeders in developing countries may concern themselves at the present time mostly with breeding for high yield and adaptation, resistance to pests and diseases, and to a limited extent, a few important quality attributes.

A slightly more detailed treatment of these breeding problems is given here, especially those relating to yield and adaptation, and resistance to two major diseases namely; late blight and bacterial wilt. Most programs in developing countries of the tropics have focused their attention to these problems (Anon, 1972). Available information did not indicate any major quality attribute under consideration elsewhere in these countries except the usual selection for the desired ideotypes of external appearance. These traits are, however, easily dealt with in breeding programs and need no extensive treatments here.

The distinct categorization of the breeding problems in this section should not give the notion that autonomous programs for each are realistic. In some cases, special emphasis perhaps may be given to some problems especially those which have proved difficult to solve, but eventually, all major objectives are integrated in the process of developing improved varieties.

5.1.4.7.1 Breeding for late blight resistance

No other disease of potato has probably wreaked more destruction on the crop, incited more fear in growers, and consequently, received more attention from scientists, than late blight. The blight epidemic of the 1840's in Europe which led to the infamous Irish famine provides glowing historical evidence to the notoriety of this disease.

The causal fungus, *Phytophthora infestans* (Mont.) de Bary, is so aggressive that if favorable conditions for its growth and sporulation continue, the disease progresses from the leaves to the haulm until this is completely destroyed, oftentimes in less than a month (Large, 1952). In temperate countries, the fungus overwinters in infected tubers until the next cropping season. In contrast, overlapping potato croppings throughout the year and presence of alternate solanaceous hosts provide a form of survival in tropical areas.

Late blight can be controlled by chemical means or through the use of resistant varieties. Preventive fungicidal sprays working hand in hand with efficient blight forecasting, sanitary practices such as destruction of discarded infected tubers and volunteers, and legislation regulating the use of blight-free tuber stocks for planting, have been very effective in minimizing yield losses in developed countries even with the use of highly susceptible cultivars. In developing countries of the tropics where potatoes are farmed mostly on small landholdings, farmers oftentimes cannot afford to spray regularly for lack of capital and/or inavailability of materials and equipment. Moreover, potatoes in the tropical countries are mostly grown in the highlands during the rainy season-a factor which introduces a difficult dimension in controlling the disease by the use of fungicides. The use of resistant varieties thus offer the brightest promise for the control of late blight in these regions.

Table 6. Details of the Cornell program of selection among clones (modified after Fig. 4 of Plaisted, 1966)

Year	No. of clones	No. of site	Locale	No. of reps	Plot length	Between-hill spacing	No. of plants/ plot	No. of select-ions	Traits under selection
					(ft)	(inch)			
1	30,000	1	isolated field	1	3	40	single hill	1,500	Highly repeatable traits, e.g., external appearance, golden nematode resistance and after-cooking darkening
2	1,500	1	"	1	10	10	12	200	Appearance, tuber size and set, specific gravity, after-cooking darkening and chipping ability
3	200	1	commer-cial area	4	15	10	18	70	Appearance, specific gravity, after-cooking darkening, chipping ability, scab and Verticillium wilt resistance and for the first time, yielding ability
4	70	2	"	4	15	10	18	25	Same selection forces as above but selection for yield becomes predominant
5	25	3	"	5	20	10	24	10	Further selection for yield
6	10	4	"	5	2x20	10	48	3-5	Same as above but in larger plots and more locations
7	3-5	6	"	4	2x20	10	48	3-5	Same as the above but in more locations; to accommodate increase in locations, reps within locations are reduced
8	3-5	6	"	4	2x20	10	48	0-2	Repeat of year 7 trial for better sampling of locations and seasons
9	0-2	6+	"	4	2x20	10	48	0-2	Repeat planting of surviving selections in 6 regional locations, in addition, separate evaluation trials where selections are most appropriate are conducted
10	0-2	6+	"	4	2x20	10	48	0-2	Same as above

11	0-2	6+	"	4	2x20	10	48	0-2	Same as above;after the year 11 trial, preparations for subsequent release of best clones are made

Two different genetic systems control late blight resistance. The first type, conditioned by a series of major genes (so-called R-genes) imparts a hypersensitive reaction in the host causing the cells surrounding the initial point of pathogen invasion to die. This reaction effectively localizes the pathogen to the area of its initial entry and subsequently is unable to survive. The major R-genes come from the wild hexaploid species, *S. demissum*, widely distributed in Mexico. There are so far 11 known R-genes, designated R_1 to R_{11}.

Black (1952) and Black et al (1953) worked out the genetical basis for classifying races of *Phytophthora infestans* based on the specific gene-for-gene relationship between the major resistance genes in the host and the virulent factors in the parasite. Accordingly for example, a variety such as Kennebec which carries the gene R_1 is resistant to races 0,2,3,4, but susceptible to races 1, 1.2, 1.3 and on (as long as the complex race carries the virulence factor able to overcome the resistance of gene R_1). Resistance, in other words, is specific to a particular race.

The major R-genes have been very useful in providing clean potato crops until new races able to overcome them evolve. Experience shows that this form of resistance is quite unstable. Clones with two or more R-genes have been bred but a new race always comes along in a few years to make the clones practically useless. The extreme variability of *P. infestans* no doubt makes the use of race-specific form of resistance only of temporary value. For this reason, breeders have now shifted to the use of another form of resistance called "field resistance" (or horizontal, non-race specific, general resistance).

Black (1970; 1972) defined field resistance as the "degree of resistance exhibited by a plant to all races of the parasite". It is inherited in polygenic fashion and various minor genes involved appear to supplement each other in the control of the disease. In individual plants, these minor genes determine : degree of resistance to infection, rate of disease spread after infection, the time required for the onset of sporulation, and the number of spores produced.

Based on the reaction of seedlings tested under controlled conditions, five resistance groups may be identified according to the amount of damage seven days after inoculation (Black, 1970). Using the system, Black (1970; 1972) was able to show that when both parents are group 1 types, the proportion of group 1 and group 2 seedlings are generally much higher, even reaching a combined proportion of 70% in some progenies (Table 7). Since these reaction types do not normally require protective spraying, the proportion of resistant seedlings available for selection of commercially important attributes is satisfactorily high.

Wild Mexican species such as *S. demissum, S. phureja, S. verrucosum, S. bulbocastanum, S. pinnatisectum, S. cardiophyllum* and *S. trifidum* have been indicated as the best sources of field resistance. *P infestans* originated in Mexico and adjacent areas, and the long, intimate association between the host species and the highly variable parasite there must have provided the best opportunity for natural selection to develop the gene pool necessary for stable resistance. Of the above species, *S. demissum* appears to have the best prospect because it crosses readily with *S. tuberosum* and, as indicated earlier, has been widely used by plant breeders throughout the world as source of R-genes. The resistance

among some of the other species may not be easily utilizable on the other hand because of their barriers to hybridization with *S. tuberosum*. Hermsen and Ramanna (1973) have provided however some hope in the hybridization work with *S. bulbocastanum*. A fairly low level of field resistance is also available in some species from South America, e.g., *S. tuberosum* ssp. *andigena, S. phureja, S. commersonii, S. acaule, S. spegazinii, S. curtilobum*, and others.

The multigenic control of field resistance and its complex expression counteract the flexibility in the aggressiveness of *P. infestans* (Umaerus, 1973). As a result, resistance is more long-lasting and stable than the race-specific resistance. Experience from the long term field testing in Toluca Valley, Mexico (an area where a complex of races is present and the only place known where sexual hybridization in the pathogen exists thus providing it with a very important mechanism for genetic change in response to the change in the host) has indicated no sudden changes of field resistance.

Table 7. Blight resistance in hybrid progenies (selected from Tables 2 and 3 of Black, 1972)

Reaction of parents[a]	No. of seedlings tested	Distribution (%) in reaction groups				
		1	2	3	4	5
1+x4-	202	4	16	33	29	18
1 x2+	210	10	6	22	38	24
3 x1	145	17	12	32	33	6
1 x3	167	12	24	25	35	4
1 x1+	125	22	46	14	10	8
1 x1+	131	17	56	15	10	2
1 x1	137	36	33	16	12	3
1 x1	180	28	41	23	6	2

[a] Group 1: restricted lesion, 3% area infected=highly resistant
2: partly restricted, 10% area infected=fairly resistant
3: retarded lesion, 30% area infected=slightly resistant
4: normally progressive lesion, 60% area infected = normally susceptible
5: rapidly progressive, 100% area infected = very susceptible
- : indicates that the reaction is on the resistant side of group while;
+: indicates that the reaction is on the susceptible side.

While stability of field resistance is an attribute that breeders ideally look for, the very fact of its complex manifestation and polygenic control make it a difficult trait to breed for. Large numbers of individuals need to be handled and hence, a practical, yet effective screening method is an essential requirement. Umaerus (1970) developed a screening test based on the finding that plants with low infection frequency also require a long inoculation access period (period of free water on the leaf surface and optimum temperature for spore germination and penetration). This character is apparently manifested in the seedling stage. Screening techniques emphasizing certain post-infectional factors, (e.g., fungal growth rate, rate of necrosis, generation time, and sporing capacity) have been used by other workers (Estrada and Guzman, 1969, Black, 1970; Young *et al*, 1972). In these methods, visual disease index measurements of disease progress serve as the selection criterion.

As may also be expected from the nature of genetic control, the expression of field resistance is highly influenced by non-genetic factors such as ontogenetic development of the plant, daylength, light intensity, and mineral nutrition. For example, blight tests for field resistance in Mexico, where photoperiod is short, using clones developed for the long days in temperate countries are often found to be too severe. Materials are ranked as more susceptible under short day conditions than they are under long day conditions. Nevertheless, breeding field resistant clones adapted to short days and higher temperature is not necessarily precluded as experienced in Kenya (Black, 1972). Late maturity and field resistance also appear to be correlated but does not preclude the combination of early maturity and resistance. The predisposing effects of increased potassium and decreased magnesium levels on certain resistance components such as lesion growth and sporulation intensity have also been reported by several workers (cf. Umaerus, 1973). High nitrogen nutrition is also associated with increased resistance under certain conditions. Broadly speaking, the influence of various environmental factors on field resistance clearly stresses the need to maintain as uniform conditions as possible during the screening period in order that genetic differences among clones are reasonably accentuated.

Breeding for field resistance can be easily complicated by the presence of major R-genes. To avoid this difficulty, breeders must either work on clones without a known major gene or test the breeding materials in locations where many races are present. The latter should enhance the chance that compatible races of the fungus matching the possible R-genes in the breeding materials exist. As already noted, such a place is the Toluca Valley in Mexico. Indeed, breeding for field resistance has been greatly facilitated using the facilities in that site (Niederhauser and Cobb, 1959; Cervantes, 1965; Lapwood, 1971).

Resistance to late blight in the foliage appears to be positively correlated with that in the tuber. Still, there are quite a large number of varieties with susceptible foliage but moderately resistant tubers. On the contrary, Howard (1978) noted that many cultivars with major R-genes for foliage resistance have very susceptible tubers.

Breeding for tuber resistance has been largely neglected although a substantial degree of varietal differences exists (Cox and Large, .1960). Part of this apathy comes from the difficulty of developing a reliable and practical screening method. Techniques of evaluating tuber resistance requiring few replicates have been devised-one method measures the frequency of infection after inoculation either by spraying whole tubers or pipetting the inoculum into the eyes while another measures the rate of mycelial growth through the internal tuber tissues. Langton (1972) claims good correlation with field resistance when tuber resistance is adjudged through a combination of the two methods. The criterion of resistance was the frequency of infected cores of tuber slices inoculated through wounded eyes combined with the average time it takes the fungus to appear on the uninoculated surface.

Umaerus (1973) emphasized the need to breed varieties with late blight resistance both in the foliage and the tuber. This is especially critical if the variety bred carries field resistance in the foliage-a situation where the pathogen is sustained for a longer period in the plant, thereby increasing the possibility of extensive damage to the tubers if tuber resistance is not present.

5.1.4.7.2 Breeding for bacterial wilt resistance

Bacterial wilt caused by *Pseudomonas solanacearum* (E.F. Smith) is common in many tropical and subtropical countries (Thurston, 1963). The disease can develop very rapidly

and be very destructive especially when temperature, rainfall, and relative humidity are favorable for its development. Crop losses of 100% are not uncommon and it is estimated that, were the disease to be controlled, potato cultivation would be increased ten-fold (Robinson, 1968). Bacterial wilt attacks not only potato but also other solanaceous and non-solanaceous crops such as tomato, tobacco, peanut and banana (Quiñon *et al*, 1964; Lozano and Sequeira, 1970; Granada and Sequeira, 1975).

Three distinct pathogenic races are recognized-race 1 attacks tobacco, tomato, eggplant, potato and other solanaceous crops; race 2 causes wilt in banana and *Heliconia* sp. but does not attack potato; and race 3 is pathogenic to potato and tomato but weakly pathogenic to other solanaceous species. Thus, only race 1 and 3 attack potato in nature. Race 3 is common in the highland tropics and can cause disease at a lower temperature threshold than other strains (Thurston, 1963). On the other hand, race 1 is widespread in both tropical and subtropical lowland areas (Sequeira and Rowe, 1969).

Effective and economical means of controlling bacterial wilt, apart from long-term cultural practices as crop rotation and field sanitation, have not been developed so far. Resistant varieties still offer the most economical way to minimize its destructiveness. Useful levels of resistance have not been found until Thurston and Lozano (1968) discovered that certain clones of Colombian *S. phureja* showed high levels. Resistance, however, is apparently uncommon—only 6 resistant clones were identified out of 1,061 tested. Sequeira and Rowe (1969) confirmed the resistance of the above clones against 10 isolates of *P. solanacearum* in greenhouse and growth chamber studies. The reaction of clones ranged from resistance to only one isolate (K-60) up to resistance to all isolates.

Recent breeding efforts have concentrated mainly on the transfer of *S. phureja* resistance to *S. tuberosum* although occasional resistance has also been reported in other species (Robinson, 1968; Thung, 1947). It appears that resistance can easily be incorporated to *S. tuberosum* (Gonzales *et al*, 1973; Rowe and Sequeira, 1972). However, resistance of clones varied not only with the virulence of the isolates of *P. solanacearum* (Gonzales *et al*, 1973) but also with temperature, varieties being more susceptible at higher temperatures (French, 1972; 1973). Table 8 clearly demonstrates the variation in cultivar reactions across different isolates and temperature regimes.

It can be seen that cultivars 1386.15 and 1386.26, both *S. phureja* cultivars from Colombia, were the most resistant across all isolates although they showed only tolerance at warm temperature regimes to the two most virulent isolates, S 213 and P1. It is worthy to note that these virulent isolates originated from tropical countries-S 213 was collected from Paraiso, Costa Rica and P1, from Chiquirip, Peru. On the other tand, less virulent isolates such as S 245 and K 51 came from temperate countries, Australia and United States, respectively.

The apparent ease with which the transfer of wilt resistance from *S. phureja* to *S. tuberosum* has been accomplished owes a great deal from the fairly simple genetic control of the character. Rowe and Sequeira (1970) concluded that resistance (to isolates K 60 and S 213) in *S. phureja*, based on reaction of diploid hybrid progenies from crosses between resistant and susceptible clones, is controlled by two dominant and independent genes for each isolate and by a common gene. This result is largely corroborated by genetic studies at the tetraploid level using as resistant parents, one 4x derivative clone from the cross *S. phureja* with *S. tuberosum* and an unrelated clone selected from the University of Guelph populations (Opeña *et al*, 1979; unpublished). Field tests of progenies derived from *S. phureja* (2x) x *S. tuberosum* (various dihaploid and tetraploid clones) also showed that high

Table 8. Reaction[a] of potato cultivars inoculated by soil infestation with isolates of *P. solanacearum* after incubation for 29 days at two temperature regimes (adapted from Table 1 of French, 1972)

		Cultivars					
Isolate	Temp. °C	1386.15	1386.26	V-7	6-5	59.B5-1	BR-6014
P1	28/16	T	T	S	T	S	S
	20/ 8	T	R	T	R	R	S
S 207	28/16	R	T	R	T	S	T
	20/ 8	R	R	R	R	R	R
S 213	28/16	T	T	S	S	S	S
	20/ 8	R	R	T	T	T	S
K 51	28/16	R	T	R	T	R	R
	20/ 8	R	R	R	R	R	R
S 245	28/16	R	R	R	T	R	R
	20/ 8	R	R	R	R	R	R
K 197	28/16	R	T	R	T	R	T
	20/ 8	R	R	R	R	R	R
K 56	28/16	R	T	T	T	S	S
	20/ 8	R	R	R	R	S	T

[a] R = resistant; T = tolerant; S = susceptible

levels of resistance have been transferred from *S. phrueja* ; indirect proof that resistance is rather simply inherited (Anon, 1974).

Results of previous studies (Sequeira and Rowe, 1969; Rowe and Sequeira, 1970; Rowe *et al,* 1972) imply that resistance to bacterial wilt may be race-specific (analogous to the major R-genes for late blight resistance). If so, there exists the danger that resistance may not be stable vis-a-vis a variable pathogen. Using epidemiological techniques based on van der Plank's (1963) analysis of plant disease epidemics, Robinson (1968) found clones which appear to exhibit vertical (race-specific) resistance, horizontal (non-race specific) resistance, or both. Based on a number of considerations such as high rate of stabilizing selection in *P. solanacearum*, its simple interest rate of increase, and its possibly high vertical mutability, it was further concluded that vertical resistance may remain agriculturally valuable for one growing season only but, given the proper rotation and use of wilt-free seeds, it would, in a wider sense, endure indefinitely. While Robinson (1968) dismissed his results as preliminary, there seems little doubt that vertical resistance to *P. solanacearum* does occur in potatoes.

The question as to which type of resistance would be most useful to combat bacterial wilt obviously needs more thorough investigation. If its analogy to the late blight situation is complete, then the sad experience with late blight will show that horizontal resistance is the most rational goal. The accompanying difficulties of breeding horizontally resistant clones will have to be taken into account by breeders. Where management practices such as effective rotation and regulated use of clean seeds can be enforced, the relative ease of breeding for vertical resistance may be enough to offset its disadvantages.

5.1.4.7.3 Breeding for high yield and adaptability

There is a definite truism to the statement that one of the best ways to develop high yielding cultivars is to breed for disease and pest resistance. However, quite apart from abiotic factors, yield *per se* is a distinct character resulting from a number of interacting yield components and consequently, quite complex in expression, under polygenic control, and easily prone to environmental effects. Pests, diseases, and other abiotic factors only serve to influence the final expression of yield. Yield, as a breeding objective, is therefore one of the most difficult that breeders have to contend with.

Simmonds (1969) considered two basic requirement in designing a potato breeding program after realism in the choice of objectives has been exercised—first, breeders need a rational choice of parents and breeding patterns, and second, efficient selection methods should be available. When dealing with oligogenically controlled characters, the known methods are fairly straight-forward and they are relatively easy to deal with. But many economical characters, including yield, are polygenic and of which, the biometrical genetic bases are rather limited, apart from being too complicated. By necessity, much of the choice of parents therefore proceed largely by instinct-"crossing the best with the best and hoping for the best".

Potato breeders work in either of two directions. They may cross an elite clone with a wide range of other clones and assume that the common parent has a fairly high level of general combining ability. In another case, specific combining ability is assumed and breeders usually explore a large number of crosses and then keep only the promising few for further exploitation. Progeny testing methods to detect variation among clones in combining ability are of course now available. Further biometrical genetic investigations of the economical characters in potato should serve to provide breeders with more guidance in the choice of best breeding approaches.

Selection techniques for yield or other complex characters in potato have been discussed earlier (Section 5.1.4.6.2). The sequential method of selection generally practised by potato breeders i.e., taking the highly heritable characters first during the early stages of selection and the complex ones later, is not only realistic but also logical. Engel (1957) pointed out the fallacy of selecting for yield and other complex characters in the seedling generation and in small clonal families. An ideal selection method when several traits are simultaneously considered is through the use of a selection index which often takes into account an economic weight for each trait under selection. However, this approach is dismissed by many potato breeders as too impractical and laborious to be a realistic procedure.

Potato generally behaves as an outbreeder although self-fertilization is possible. Successful clones, almost automatically those with high yield and good adaptability, are highly heterozygous and presumably heterotic. Breeding methods to improve yield and adaptation is therefore geared towards attaining maximum heterosis in breeding populations in order that chances of recovering outstanding clones are improved. Experience with other crops such as maize and the theory of gene action indicate the importance of genetic diversity for greater manifestation of heterosis.

By and large, the total potato breeding effort in temperate countries has increased enormously since 1910, the acknowledged end of the heyday of potato breeding. Although some notable variety releases have been made since, e.g. Katahdin in USA, Ackersegen in Germany, Voran in Holland, Arran Pilot in England, and a few others, Simmonds (1969) considered the accomplishments of modern breeding incommensurate to the overall scientific

inputs to potato improvement. The narrowness of genetic diversity in Tuberosum breeding stocks has been pinpointed as the major limitation. More recent potato breeding efforts have emphasized the infusion of genetic diversity into the current Tuberosum gene pool and the use of the Andigena group for this purpose has received the greatest attention.

The Andigena potatoes are short-day adapted types. When grown during the long, summer days of temperate countries, they tend to be late-maturing and unproductive. Moreover, they generally show poor tuber shape, deep eyes, poor resistance to diseases, excessive vine growth, narrow leaves, poor canopy, etc. Nonetheless, it is now widely recognized that the present day Tuberosum gene pool evolved from a limited introduction of Andigena clones into Europe during the early part of the 16th century (Salaman, 1946; Salaman and Hawkes, 1949; Salaman, 1954) and is a magnificent tribute to its enormous store of genetic potentiality for improvement.

Because of the undesirable features of Andigena potatoes, Andigena (A) x Tuberosum (T) hybrids almost invariably result in a low frequency of selection but a higher potential for yield. In order to enhance the commercial potential of AT hybrids, preliminary selection in Andigena is needed to remove the undesirable portion of variability (Glendinning 1969). AT hybrids using unselected Andigena are generally too late to reach their yield potential. Thus, although heterosis is theoretically maximum in the immediate F_1, some sacrifice in terms of accompanying loss of heterosis (brought about by progressive narrowing of variability due to selection) is a necessary compromise in order that variation in AT hybrids will overlap with commercial requirements. Just how much this sacrifice will be remains to be seen. Using selected Andigena clones in crosses with Tuberosum, the mean progeny advantages of AT hybrids over intra-Tuberosum hybrids tested in temperate regions were still impressive (Glendinning, 1969; Cubillos and Plaisted, 1976; Tarn and Tai, 1977). Thus, the predicted heterosis in yield expected from infusion of variability from Andigena to the Tuberosum gene pool is unquestionably there to exploit.

The basic objection to the utilization of Andigena in previous breeding efforts in temperate regions, apart from its lack of adaptation to long days, is its extreme susceptibility to diseases, notably late blight. The mass selection programs in Andigena populations at Pentlandfield, Scotland (Simmonds, 1969) and at Cornell University (Plaisted, 1972) have not only yielded advanced clones with yielding capacity and maturity that are comparable with Tuberosum clones but, on the average, they are somewhat better in terms of late blight resistance. For example, the 5th cycle of the Cornell population tested in Toluca, Mexico in 1973 showed 37% with high levels of field resistance. The variability of Andigena populations has also yielded clones with resistance to PVY, PVX, common scab, *Verticillium* wilt, aphids, leafhoppers, golden nematode, root knot nematode, etc. The progress that had been achieved in the Andigena selection program and their exciting breeding possibilities offer the present-day potato breeders a broad new horizon to improve potatoes beyond the levels attained by their 19th century predecessors.

The continuing use of mainly Tuberosum cultivars for potato improvement in developing countries has been suggested earlier as a potentially unrewarding approach (Section 5.1.1). While it is true that most successful cultivars in many of these regions are Tuberosum types (especially late maturing maincrop varieties of the temperate zones), the prospect of further replacing them with more highly selected Tuberosum clones from local or foreign breeding programs is not good in view of the limited genetic diversity of the Tuberosum gene pool. In its stead, the utilization of Andigena gene pool and the hybrids of preselected Andigena clones, or Neotuberosum in Simmonds' (1969) terminology, with

locally adapted Tuberosum cultivars may very well be a more productive approach. Simmonds (1971) even ventured to suggest that major efforts to adapt the potato to a climate different from its own habitat, e.g., hot, humid tropics, should look at the useful genetic variability in Andigena rather than attempt to find adapted types from highly selected Tuberosum clones. If the new regions are marginally suited to Tuberosum, the use of hybrids between Tuberosum and selected Andigena clones may provide the greatest opportunity for success (Plaisted, 1972).

5.2. Non-traditional breeding methods

Although almost all *S. tuberosum* cultivars grown today have been developed through conventional breeding (introduction, hybridization and selection), an exceptional few arose as bud sports (somatic mutation) from established varieties and have since been adopted by farmers whenever they were found economically important. For example, Howard (1970) estimated that in 1968 in England, there were 20,000 acres grown to Red Craigs Royal compared to about 6,000 acres of its original type, Craigs Royal. Other examples of bud sports that have become established cultivars are Red Pontiac, derived from variety Pontiac, and Red La Soda, which originated from variety La Soda (Anon, 1967).

In addition to mutation breeding, new methods and other exciting areas of development are being explored by potato scientists around the world. The potential use of dihaploids in breeding has occupied much research attention since the pioneering work at Wisconsin of Hougas and Peloquin (1958) on generating them in higher than normal frequencies. The use of botanical seeds in actual commercial production instead of tubers has recently received some research impetus. This has an obvious potential for developing countries without a good seed program. Apart from these, more sophisticated approaches such as protoplast fusion are opening new vistas for further potato development.

It is the purpose of this section to present relatively briefly these non-traditional methods in order to broaden the perspectives of researchers engaged in the field of potato improvement and update their knowledge of the scientific developments therein.

5.2.1 Potential use of dihaploids in potato breeding

Dihaploids are diploid plants derived through parthenogenesis from tetraploids. Potato dihaploids (2n=24) have been known since the 1930's but they occurred rather infrequently. It was not until the discovery of Hougas and Peloquin (1958) that certain diploid *S. phureja* pollinators on female tetraploid Tuberosum and Andigena clones can increase their frequency that interest on the potential use of dihaploids in breeding was greatly intensified.

Later studies (Peloquin et al, 1966) showed that the dihaploid frequency can be further increased by using the cut stem method for flower production and subsequent pollination in the glasshouse (see also Section 5.1.4.4), and by choosing superior pollinators from *S. phureja*, particularly Pollinators 1.1, 1.3 and 1.22 selected from *S. phureja* clone PI 225682. Hermsen and Verdenius (1973) improved the method further by using a genetic marker, embryo spot, which facilitated the identification of dihaploids from 4x-2x crosses.

Hougas *et al* (1964) observed that selected pollinators can give dihaploid frequencies of about 10 per 100 berries in crosses with a wide range of female parents in contrast to an average for other pollinators of only one dihaploid per 100 berries. Hanneman *et al* (1978) observed more or less comparable frequencies (13 dihaploids per 100 berries) from Group Andigena. The superior pollinator effect appears to be simply inherited with either one or a few recessive genes involved (Peloquin *et al,* 1964).

The influence of female parents on frequency of dihaploid production is also significant, clones such as Merrimack and Wis. Ag. 231 averaging 10 dihaploids per 100 fruits compared to just over one for other seed parents (Hougas *et al,* 1964). Frandsen (1967) observed an interaction however between seed parents and pollinators.

When tetraploid seed parents (4x=48) are pollinated by *S. phureja* diploid pollinators (2n=24), it is expected that triploid progenies (3n=36) will be produced, However, results showed that these triploids are produced in surprisingly low numbers, the majority being tetraploids (arising from fertilization of 2n egg cell of tetraploid seed parent by unreduced 2n pollen of the pollinator) and the minority are diploids. There appears to be a triploid block in 4x-2x crosses (Marks, 1960). The diploids (or dihaploids, in the sense that they are haploids of tetraploids) have been genetically shown to be maternal in origin, derived from unfertilized egg cells which developed parthenogenetically. Further studies (Wangenheim *et al,* 1960; Bender, 1963) showed that dihaploid embryos (24 chromosomes) were regularly associated with hexaploid endosperm (72 chromosomes) instead of the expected pentaploid endosperm (60 chromosomes). Based on indirect evidence, it has been suggested that a superior pollinator is one which contributes two 12-chromosome male gametes leading to the development of hexaploid endosperm (48+12+12=72 chromosomes). In the process, no male gamete is available to fertilize the egg cell (24 chromosomes). Parthenogenetic development of these unfertilized egg cells thus gives rise to dihaploid plants.

Dihaploids are generally weak (Wohrmann, 1966) as may be expected from the genetical consequence of their derivation—generating dihaploids from tetraploids is equivalent to three generations of inbreeding the tetraploids. Krantz (1946) showed that tetraploid potatoes behave genetically as an outbreeder and exhibit inbreeding depression upon selfing, although at a rate slower than inbreeding of diploid species. Occasionally, some dihaploids appear to be as productive and vigorous as their parents. Hybrids between Tuberosum dihaploids and diploid species *S. phureja* also showed improved vigor and yield (Hougas and Peloquin, 1965; Rowe, 1967a).

Most dihaploids are pollen sterile but a great majority have been found to be slightly female-fertile. Caroll and Low (1975) observed considerable reduction in female fertility of first generation dihaploids of *S. tuberosum.* In some cases, dihaploids also produced flowers with some difficulty. For example, of the first 60 dihaploids produced, 53 flowered of which 30 were female fertile but only 5 had viable pollen (Ross *et al,* 1964). Pollen infertility obviously may be a serious barrier to the utilization of dihaploids. However, crosses between dihaploids with other diploid species or among themselves can increase not only pollen fertility but also vigor and productivity of the resulting progenies (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a; Tiemann, 1976). There are also indications that dihaploids from Group Andigena have better male and female fertility than those from Tuberosum (Landeo and Hanneman, 1979).

Several methods have been proposed to use dihaploids in potato breeding. Hougas and Peloquin (1958) presented most of the arguments in favor of doing the genetic and breeding studies at the diploid level as contrasted to the tetraploid level. Chase (1963) suggested a ten-step analytical breeding scheme where intensive inbreeding and selection are done at the diploid level followed by resynthesis of the tetraploid forms. The evidence on the question of the need to return to tetraploid level for commercial production is conflicting.

Rowe (1967) compared 11 diploid with 11 tetraploid hybrid families and concluded that gene action and heterozygosity may have a greater influence on vigor and productivity than ploidy level. The tetraploid hybrid families (from *S. phureja* x Tuberosum dihaploids)

yielded better than diploid families when established from botanical seeds. However, this advantage disappeared when both were propagated from tubers. Diploid families also showed greater variability which indicated that they could respond to selection faster than tetraploids. In another paper, Rowe (1967b) found that diploid clones from *S. phureja* x Tuberosum dihaploids generally performed better than their vegetatively doubled counterparts.

On the other hand, Mendiburu and Peloquin (1971) produced tetraploids via sexual polyploidization (4x-2x and 2x-2x crosses in which unreduced gametes functioned) instead of vegetatively doubling the chromosome number and found that these clones outyielded their diploid "full sibs" by 50 percent. Chase (1963) suggested the resynthesis of tetraploids via unreduced gametes as an alternative to vegetative doubling. Sexual polyploidization does not involve inbreeding while vegetative doubling is approximately equivalent to two generations of selfing a tetraploid (Haynes, 1972). Thus, Rowe's (1967a) data indicating the inferior performance of the vegetatively doubled counterparts of diploid clones may have been largely due to inbreeding depression.

Regardless of the above controversy, the relative genetic simplicity of dihaploids compared to tetraploids and its consequence in genetical and breeding work is an overwhelming opportunity that potato scientists should attempt to exploit. However, if potato breeding is to be carried out at the diploid level, there is an urgent need to assemble the necessary diploid parents, particularly since the fertility of dihaploids is low and selection for fertility as well as for the desired characters have to be done (Howard, 1978). This problem appears to be surmountable as intercrosses among dihaploids or their crosses with cultivated *S. phureja* do show improved vigor and fertility (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a; Howard, 1970; Tiemann, 1967).

With regards to crosses of dihaploids with other diploid species, Simmonds (1966) argued that any population of Tuberosum dihaploids is genetically narrow-based like their source gene pool and so would have little potential for improvement ; therefore, a program of infusing genetic variability from diploid species into the population of Tuberosum dihaploids along the line of the Andigena program is clearly necessary. Already, mass selection programs among widely based South American diploid stocks are underway (Simmonds, 1969; Haynes, 1972) so that eventually, more commercially desirable hybrid progenies between these improved diploid stocks and the Tuberosum dihaploids may be possible to select. Haynes (1972) pointed out, however, that direct utilization of improved diploid cultivars, particularly those from cultivated species *S. phrueja* and *S. stenotomum*, should not be neglected. Most of the diploid clones grown commercially in South America are largely unimproved and its great potential for production has heretofore been unexploited. He cited not only the more rapid response to selection expected on diploids as a major advantage but also the opportunity of isolating more productive genotypes for specific environments.

Even assuming that breeding at the diploid level will turn out to be not as promising as everyone hopes, the synthesis of useful tetraploid breeding stocks via dihaploids should have immediate significance (Simmonds, 1969; Howard, 1970; Howard; 1978). For example, a dihaploid clone carrying a dominant gene for resistance (either in single or double dose) can be vegetatively doubled using colchicine to produce tetraploid stocks which carry that particular gene in duplex or quadruplex form, as the case may be. Using such stocks in breeding at the tetraploid level, rather than the simplex clones more commonly available to the breeder, provides considerable gain in efficiency. It can be shown easily that quadruplex and duplex stocks crossed with nulliplex clones will yield 100% and 83% hybrid progenies with

the desirable dominant gene, respectively. In contrast, simplex clones in similar crosses will give only 50% desirable progenies. This argument has been extended by Howard (1978) to relatively more complex quantitative characters. Clearly, the number of progenies to handle in the breeding program can be significantly reduced using such specially synthesized stocks. There are indications that improved levels of disease resistance can be found among dihaploid stocks (Alam and Peloquin, 1971; Cipar and Lawrence, 1972; De Maine, 1978). Therefore, synthesis of special tetraploid stocks is a possibility.

5.2.2 Mutation breeding

Mutation can be roughly described as heritable genetic changes either occuring naturally (spontaneous mutation) or artificially induced (induced mutation) by mutagenic agents such as radioactive rays or chemicals. As mutation contributes to genetic variations which serve as the raw materials for selection, their potential use in breeding has also been explored in some crop species. Stebbins (1950) considers mutation as the ultimate source of variation between two individuals.

In potato, a few cases of bud sports (somatic mutations) that have led to the development of commercially accepted cultivars have been cited earlier. Artificial induction of mutations as a tool in potato breeding has not been generally well accepted, however, even though the methods have greatly developed since the discovery as early as 1935 by Asseyeva and Bladigova that X-ray can provoke mutations in potato. Now, mutations in potato can be induced by a wide range of agents : physical agents apart from X-ray are P^{32}, gamma rays, and more recently, neutrons (Solomko, 1965; MacCrory and Grun, 1969; Van Harten, 1972; Gomez Cuervo and Estrada, 1972; and Miedema, 1973); chemical agents such as ethyl methanesulfonate (Ferwerda, 1965; Umaerus, 1966); ethyl imine, diethyl methanesulfonate, N-nitrosomethylurethane, etc. (Nayar and Chauhan, 1968; Jauhar, 1969; Pavek, 1972; Upadhya and Purohit, 1973).

The lack of interest in induced mutation as a breeding tool in potato may be attributed to prejudices, irrelevant arguments, and a considerable amount of conservatism among potato breeders and some scientists (Van Hartin, 1978). Nonetheless, he did admit that, 40 years after the discovery of mutation-inducing ability of X-rays in potato, not much has been achieved in practise. Notable exceptions are the release of cv. Konkei 45 with improved tuber skin color in 1973 in Japan and the reported release to Soviet farmers of some cultivars with improved resistance to late blight derived from gamma-irradiation (Anon, 1973).

Several reasons have been given to account for the lack of success of mutation breeding (Van Harten, 1978). Technical problems always appear foremost in the argument. If mutation breeding is to be a practical tool in potato improvement, many diverse mutations must be produced and if they can be obtained, the method may seem at least as promising as handling thousands of hybrid seedlings (in conventional breeding) of which really only a few or even none leads to a new cultivar. It has been proven by several workers (Heiken, 1960; Anon, 1963; Nayar, 1969; Nayar and Dayal, 1970) that high frequencies of induced mutations can be obtained. For example, Heiken (1960) obtained 37% mutated plants at a dose of 2,000 - 3,000 R of X-rays but even as high as 50% is achievable (Nayar and Dayal, 1970) by periodically removing and separately planting the sprouts from irradiated tuber halves. From these results, low frequency of induced mutations cannot be the limiting factor in the practical application of mutation technique.

It appears that the term "mutation" has also acquired an unfortunate connotation of undesirableness, products being considered aberrants (or deviation from normal). To some

extent, this prejudice does have some legitimate basis in the sense that the most visible mutations in many crop species either are deleterious or if not, carry with them some undesirable pleiotropic effects (in practise, pleiotropy and extremely tight genetic linkage are difficult to distinguish). The reports on the frequency of desirable mutations in potato are conflicting. For example, Asseyeva and Yashina (1968) concluded that only 6 or 200 induced mutations they examined in potato had some practical value and of the 6, only one was found in a commercial cultivar. On the other hand, Solomko (1962; 1965) claimed that only 4 - 8% of induced changes obtained are adverse types. Even 17% of mutants produced in some well known Russian cultivars were reported to be useful, some of which were suitable for direct practical use. Van Harten (1978) surmised that the effect of pleiotropism is less important than anticipated before and assuming that high quantities of mutations can be induced, types without negative side-effects undoubtedly can be found.

The other reason for the lack of success in applying mutation breeding is the tendency of many mutation breeding experiments to dwell on rather preliminary trial stages (Van Harten, 1978). Many experiments were on limited scale and only for a few vegetative generations. In some cases, it is difficult to determine, especially when work was conducted with very limited vegetative generations, whether the reported mutation is real or due to primary injury or physiological damage incurred by mutagenic agents. Non-hereditary effects should be ideally set apart from hereditary changes. In mutation experiments, only healthy and virus-free plant materials (virus symptoms have often been mistaken for mutation) should be used and this point has been neglected by many investigators.

Ideally, mutations of a non-chimeric nature, i.e., 100% solid mutation, is highly preferable in breeding. With vegetatively propagated species such as potato, the multi-layered structure of the shoot apex and of tissues derived from it enhance the development of a single cell mutation into a more or less stable periclinal chimera (Jorgensen and Crane, 1972). Chimeric plants are those composed of both mutated and non-mutated somatic cells or tissues. Depending upon which histogenic layer these mutated cells occur, they may or may not be possible to regenerate. Only mutations that are possible to regenerate are useful in breeding. For example, some bud sports cannot be reproduced generatively (by seed) because the mutation occured in cell layers other than the subepidermal zone (L II cell layer). Dorst (1924) as cited by Van Harten (1978) mentioned that only mutations present in the subepidermal layer can be propagated generatively since germ cells arise only from this zone.

A method to produce high frequencies of solid mutants has been developed (Van Harten *et al*, 1972). The method employs tuber-eye plugs from which the main eyes have been removed before irradiation with high doses and dose rates. The sprouts arising from the eye region after irradiation are dissected and planted out individually. The sprouts which develop about three months after radiation treatment are mostly of adventitious origin, producing mutants which are practically 100% solid. This technique to produce chimera-free mutations is rather laborious however and it seems necessary to look for a better and quicker method (Van Harten, 1978).

Taking into account the favorable developments in mutation techniques, as well as the fact that massive, laborious conventional breeding programs do not always lead to success, Van Harten (1978) argued conceptually that mutation breeding does have a role to play in potato improvement. He cautioned however that realism must be exercised in applying mutation technique as a practical breeding tool. As long as sufficient genetic variation can be obtained more easily (such as with conventional breeding), the mutation breeding method should not be applied. The most promising approach, in Van Harten's view, is to apply the

mutation method in advanced stages of conventional breeding to cure certain, well-defined "defects" in promising breeding materials and in commonly grown cultivars.

5.2.3 Other interesting developments in the field

Potential of monohaploids

The successful derivation of dihaploids from cultivated tetraploids has its logical extension in further attempts to reduce the ploidy to monoploid (monohaploid) level. There are certain genetic and breeding implications to this approach. Of most immediate significance to the breeder is the possibility of generating completely homozygous diploids. Their use in developing potato hybrid varieties reproducible as true seeds, along the line of hybrid maize, would be a breakthrough in potato breeding with far-reaching impact (see further discussions below).

Two lines of approach have been tried in generating monohaploids of potato. The first is an extension of the parthenogenetic method used originally to derive dihaploids. Breukelen *et al*, (1975; 1977) successfully produced 85 viable parthenogenetic monohaploids (2n = 12) from *S. tuberosum* and *S. verrucosum.* All were induced using diploid *S. phureja* clones homozygous for the genetic marker, embryo spot, as pollinator. The frequency of monohaploid induction was consistent for three successive years—14,17, and 17 per 100 berries. Although none of the monohaploid plants showed male or female fertility, doubling of their chromosome number by colchicine yielded homozygous diploids with low pollen quality but good seed fertility. Other species, e.g., *S. multidissectum* and *S. berthaultii*, yielded no monohaploids suggesting that highly self-incompatible species may have accumulated more lethal genes concealed in the heterozygous condition. Of the three species tested, only *S. verrucosum* is self-compatible.

Monohaploid plants have also been produced by inducing plantlet formation in anther cultures (Foroughi-Wehr *et al* , 1977; Sopory *et al* , 1978; Weatherhead and Henshaw, 1979). Plantlets derived from anther cultures were a mixture of polyploids, dihaploids and monohaploids, majority of which are non-haploids (Foroughi-Wehr *et al* , 1977) which is often expected when plantlet regeneration occurs via calluses (Sopory *et al* , 1978). Jacobsen and Sopory (1978) observed that the genotype of the clone, apart from physical-chemical factors, is very important in the success of anther culture and that improvements may be made by selecting and recombining existing genotypes to develop clones with positive response to anther culture.

Foroughi-Wehr *et al* (1977) claimed that anther culture has the advantage over female parthenogenesis (Breukelen *et al* , 1975; 1977) in generating monohaploids on grounds that there are thousands more pollen grains than there are ovules. However, they failed to mention that dihaploid potatoes often have poor pollen fertility thus negating its advantage in number. Moreover, chimeric plantlets appear occasionally from anther culture. Plantlets from anther culture of cultivated potato have also proven to be difficult to obtain (Irikura amd Sakaguchi, 1972; Irikura, 1975). On balance then, it would appear that the female parthenogenetic method has more merit than the anther culture technique, besides being comparatively simple. However, anther culture techniques have greatly advanced that more dihaploid plantlets can now be generated (Wenzel and Melchers, 1979).

Three possible methods (Breukelen *et al* , 1977) have been suggested to double the chromosome number of monohaploids to produce homozygous diploids—via the use of colchicine, by unreduced (2n) gametes, and by protoplast fusion. Of these, the use of

colchicine is well known and needs no further elaboration. Unreduced gametes appear frequently in potatoes and may have even played a very important role in the polyploid evolution of some species (Hawkes, 1978). Protoplast fusion, on the other hand, is relatively unexplored field but advances are steadily coming.

Protoplast fusion

Protoplast fusion is essentially somatic hybridization where the intact genomes and cytoplasms of different parents are induced to fuse via their protoplasts. Interest in the field is high because of the potential for wide somatic cell fusion between distantly related plants (Nickell and Heinz, 1972). Thus far, plantlets have been successfully generated from fused proptoplasts of some plant species and fusion without regeneration on a number of others. For examples, Carlson *et al* , (1972b) isolated protoplasts of *Nicotiana glauca* and *Nicotiana langsdorfii,* fused them and isolated somatic hybrid plants by means of a selective screen system that depended on differential growth of the hybrid on a defined media. Plantlets from fused protoplasts of carrots have also been produced (cf. Nickell and Heinz, 1972).

In potato, successful regeneration of plantlets from isolated mesophyll protoplasts was reported by Binding *et al* (1978) and Grun and Chu (1978). Protoplasts from 4 of 6 dihaploid *S. tuberosum* clones regenerated into plants which had stable karyotype (Binding *et al* , 1978). Melchers *et al* (1978) regenerated somatic hybrid plants of potato and tomato from fused protoplasts. Four regenerated plants showed expression of both tomato and potato nuclear genes proving these plants to be somatic hybrids. The chilling resistance of these somatic hybrids was invesitgated by Smilie *et al* (1979). Tomato is generally susceptible to chilling temperatures whereas potato is relatively resistant. The study showed that chilling resistance of somatic hybrids was intermediate between tomato and potato, prompting the above investigators to conclude that somatic hybrids may be very useful to transfer the chilling resistance of potato to tomato.

Somaclonal variation

The potential of variation between plants generated from single cell cultures of potato has also been explored in the manner that had been done for sugar cane (Heinz, 1977 cf. Shepard, 1980) or in tobacco (Carlson *et al* , 1972a). Wenzel and Mechers (1979) cited that microspore and protoplast culture techniques to derive plantlets from *S. tuberosum* dihaploids are vastly improved—more than 2,000 microspore-derived and several hundred protoplast-derived plantlets have already been produced in their program. They proposed an extension of Chase's (1963) analytical synthetic breeding scheme whereby tetraploids are reduced to dihaploids via female parthenogenesis (using *S. phureja* pollinators); selected dihaploids carrying complementing traits are then further reduced to monohaploids with selection for appropriate traits and subsequent *in vitro* chromosome doubling; two complementing doubled monohaploids (dihaploids) are then crossed to produce diploid clones carrying the traits of both parents, after which fusion of their protoplasts is carried to create the synthetic, heterozygous tetraploids carrying all the desired characters of the four original tetraploids clones.

Shepard et al (1980) reported that clonal populations regenerated from single leaf cell protoplasts on potato cultivar Russet Burbank displayed a high frequency of variation for several horticultural and disease resistance characters. Observation over a period of three tuber generations suggested stable changes in tuber shape, yield, maturity, photoperiod requirement for flowering and plant morphology. Enhanced resistance to early blight and late

blight also regularly occurred within the regenerated populations. While the results obtained were unquestionably impressive, there were some unsettled questions, e.g. source of protoclonal (protoplast-derived clones) variation without mutagenesis—epigenetic causes, somatic mutations, or point mutations in leaf cells? It has been argued however that vegetatively propagated crops do exhibit a high degree of spontaneous somatic variation such as for example in sweet potato cultivar Centennial where two plants in 100 have been estimated to be morphologically distinct.

True potato seed for commercial production

Commercial planting of potatoes from true (botanical) seeds in place of tubers is another area of development with major implications especially for developing countries without an effective, well-organized tuber seed programs. Traditionally, raising potatoes from the true seeds is restricted mainly to the first generation after hybridization; thereafter, selected plants and established varieties are propagated by tubers. Without an effective tuber multiplication scheme, clones invariably accumulate degenerative viral diseases that significantly cause yield losses. It is probably fair to conclude that low yields of potatoes in developing countries, where lack of good seed program is more of a rule than exception, are in large part due to the use of poor, virus-infected seeds.

True potato seeds (TPS), on the other hand, are almost completely virus-free (spindle-tuber viroid is an exception since it is seed-transmissible according to Diener, 1971). Apart from the advantage in health of planting materials, growing commercial crops from TPS offer other benefits (Bedi, 1978) such as: use of TPS can reduce volume and weight of planting materials, e.g., 65 grams of TPS can plant a hectare that would require 2 tons of tubers; TPS retains viability without serious deterioration of vigor and viability (Howard, 1969; 1975; 1978; Simmonds, 1968); TPS can be stored at room temperature without physiological impairment (Howard, 1978) while tubers need carefully controlled, expensive cold store facilities; TPS can substantially reduce production cost as they are easier and cheaper to produce, light in weight thus cutting transportation and storage costs; TPS would free a major portion of land devoted to seed potato crops for production of other food crops. All in all, it is clear that TPS carries overwhelming advantages over tuber seeds. The negative points of TPS are purely technical and, with research efforts being now intensified in many parts of the world, may possibly be resolved in time.

The most obvious disadvantage of TPS is the lack of phenotypic uniformity for many characters, e.g. seedling vigor and emergence; tuber attributes such as shape, color, size, depth of eyes, etc., maturity, general vegetative growth; and even consistency in yield performance from plant to plant. Admittedly, one can argue that the requirements for phenotypic uniformity in developing countries are not as rigid as in areas of the world where potato is a major crop. However, a certain degree of yield stability from plant to plant would be desirable. A wide range of maturity of TPS could significantly alter the cropping system in place and may pose some problems. Small farm systems where multiple, sequential croppings are practised would not be favorable for TPS production because of variable and long maturity. The more visible criteria of uniformity (those relating to external tuber appearance) are without doubt the easiest to resolve from a breeding standpoint.

The genetic basis of TPS variability lies on the high level of heterozygosity in tetraploid clones. Regardless of whether TPS are derived from hybridization, selfing, or open-pollination, variability will always be released and will be evident among progenies. Apart from its heterogeneity the overall performance of TPS may not compare with tuber

propagation, e.g. smaller yield on per plant basis, smaller tuber size, fewer tubers, longer maturity, etc. Selection for important TPS traits appears possible however and evidence points to an expected rapid improvement in many of these characters (Anon, 1980b). For example, in an experiment using North Carolina Design I developed from 15 randomly selected male clones each crossed to a random sample of four female cones (all clones were derived from a Neo-tuberosum population), additive genetic variance was significant for 10 of 16 traits studied (Table 9). Yield was not considered because of its non-additive nature in the population sampled.

Table 9. Narrow sense heritability (h^2) estimates from full-sib families of several traits in potatoes propagated by TPS (after Anon, 1980)

Character	Heritability
Germination percentage	.53
Transplant survival	.30
Nursery vigor	.56
Nursery uniformity	.33
Resistance to Rhizoctonia	.55
Days to maturity	.57
Number of berries	.58
Tuber number	.60
Tuber size	.79
Depth of eyes	.57

High yield *per se* appears to be obtainable in TPS. In an experiment comparing F_1 hybrid seedlings, open-pollinated (OP) seedlings and F_1 tuber-propagated families, F_1 seedlings and F_1 tuber-propagated entries significantly outyielded the OP seedlings in one of two locations (Anon, 1980b). No significant differences were noted in another test site. F_1 and OP seedlings tended to produce smaller tubers than F_1 tuber-propagated plants. This result was explained on the basis that seedlings usually produced a large number of secondary stems by profuse branching. Selection for large tuber size of TPS should be achievable however in view of its fairly high heritability (see Table 9). Certain agronomic management such as controlling the number of branches/stems by pruning could also possibly improve the size of tuber sets in TPS. This practise is not new—Taiwanese farmers regulate stem density of commercial tuber—propagated potatoes to produce uniform, good size tubers (personal observations).

In another study, Bedi (1978) reported that one TPS line approached the yield of commercial varieties raised by normal vegetative means. Accatino (1980) observed the presence of several hybrid progenies with good yielding ability and good uniformity of tuber color and shape in a growth duration of 90 days at San Ramon, and Lima, Peru. Yields of 15-26 tons per hectare have been noted among a broad sample of TPS families (Anon, 1980b). Fifteen families were also found to be very uniform.

When the subject of high yield combined with agronomic uniformity comes to light, breeders cannot help but be reminded of the classical example of success with hybrid maize. There is no doubt that potato, being genetically an outbreeder, is highly heterozygous and exhibits significant heterosis (Rothacker, 1962; Glendenning, 1969; Cubillos and Plaisted,

1976; Tarn and Tai, 1977). Therefore, high yield through maximization of heterosis is a logical objective in TPS cultivars. The problem lies in achieving agronomic uniformity. In maize, homogeneity is achieved in the hybrids because essentially homozygous inbred parents are used in creating the hybrids. However, potato is a highly heterozygous tetraploid and any attempt to inbred clones as suggested by Krantz (1946) will be time-consuming since the approach to homozygosity is slower than in diploid crop species like maize. Moreover, few Tuberosum varieties are pollen-fertile; hence inbreeding by selfing restricts the number of inbred lines of diverse origins that can be produced (Howard, 1970).

The producion of dihaploids (see Section 5.2.1) and monohaploids (discussed earlier in the current section) provides a serious alternative to inbreeding at the tetraploid level. At the dihaploid level, De Jong and Rowe (1971) concluded that obtaining homozygous clones appears possible. The advantage of inbreeding at the diploid level in terms of a faster approach to homozygosity is clear. Assuming no selection for heterozygosity, the diploid S_5 generation is about 97% homozygous. By comparison, the same generation in an autotetraploid assuming random chromosome segregation is only 57% homozygous (Bartlett and Haldane, 1934). Krantz (1946) considered potato as an autotetraploid because its actual yield depression as percent of mean F_1 yield was lower than those calculated on the assumption that potatoes are allotetraploids.

Apparent homozygosity in diploids has reportedly been achieved via monohaploid induction followed by colchicine doubling (Breukelen *et al,* 1975; 1977). Wenzel and Melchers (1979) also cited the rapid advances that have been achieved in anther and protoplast culture techniques. In time, therefore, generating homozygous clones, be they diploids or tetraploids, should be within reach of potato breeders. The limitation appears to be in finding homozygous clones with improved male and female fertility so that they can be used in creating reproducible F_1 or open-pollinatd TPS cultivars. There are some indications that intercrosses among dihaploid clones or hybridization with cultivated diploid species can alleviate the fertility and vigor problems (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a). If this is so, producing TPS hybrids may necessitate parental stock development to improve vigor and attain high seed productivity. Careful selection of parents must be done however to insure that recovery of vigor and fertility is not done at the expense of relative agronomic uniformity.

Assuming that homozygous, good-combining diploid stocks with high fertility can be produced and a regular tetraploid TPS hybrid is desired, some limitations of the approach should be taken into account. Chromosome doubling of homozygous diploids will not alter its inbreeding coefficient ($F = 0$) but putting two doubled stocks into hybrids, each with $F = 0$, will result in progenies partially retaining some of the inbreeding of the parents ($F = 1/3$ among progenies). Thus, loss of vigor in the hybrid progenies is theoretically expected. A mechanism that might be exploited to achieve high yield and agronomic uniformity of TPS at the tetraploid level is through the sexual polyploidization process (via 2n or unreduced gametes fromed by FDR, or first division restitution). Mendiburu and Peloquin (1971) observed that the tetraploid progenies from 4x-2x matings are not only vigorous and high yielding but also uniform. Similar results were obtained by De Jong and Tai (1977; 1978). The cytological basis of 2n pollen formation which leads specifically to heterotic tetraploid progenies in 4x-2x or 2x-2x crosses, i.e., FDR through parallel spindle formation during meiosis, is simply inherited (Mok and Peloquin, 1975a; 1975b) and manifested in the pollen phenotype (Simon and Peloquin, 1976) so that it can easily be bred into dihaploid stocks. If diploid clones with good agronomic attributes, high frequency of 2n gamete formation via

FDR, and good combining ability can be found, then production of relatively uniform, high yielding TPS (with mostly tetraploid progenies) may possibly be achieved.

Summary

A review of breeding and genetics of potato has been presented here to provide the breeders in developing countries with some fundamental guidelines in potato breeding and an updated knowledge of recent developments in the field.

The survey of published articles was made as comprehensively as possible but, understandably, other important studies may have been inadvertently omitted. Part of the difficulty lies in the long history of potato as a scientific subject, a good indication of its great importance. Most of the different subjects dealt with in this chapter are replete with volumes of literature so that omission of a number of them was inevitable.

It must be mentioned that the potato breeding problems in developing countries obviously transgress those that were cited and/or implied in the present article. However, emphasis was placed only on the most common ones for the sake of giving them a slightly more comprehensive treatment.

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Breeding Leguminous Vegetable Crops

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INTRODUCTION

Leguminous vegetables have been cultivated for more than 6,000 years in different parts of the world. Legumes for human consumption constitute about 5% of the cultivated crops. World production of selected vegetable legumes are given in Table 1.

Table 1. Area and production of selected vegetable legumes in specific region and the world.

Vegetable	Country / Region	Area ha x 1000	Production t x 1000
Green Peas	World	802	4,699
	Asia	89	144
Green Beans	World	391	2,527
	Asia	102	636
Dry Peas	World	8,428	11,361
	Southeast Asia	27	22
Dry Beans	World	25,959	14,637
	Southeast Asia	1,437	1,082
Soybeans	World	52,600	96,000
	Asia	7,500	10,000

In countries like India where majority of the population is vegetarians leguminous vegetables serve as the major source of protein in the diet. In developing third world countries, especially for the poor people, the major protein source in the diet is vegetable legumes. Most of the leguminous vegetables are rich in phosphorous, calcium, iron and a number of essential vitamins. Crops like soybean, groundnut, and Bambara groundnut are also rich in fats which are essential for the absorption of vitamin A by our system. Although leguminous vegetables are deficient in some of the sulphur containing amino acids when consumed with cereals they are well compensated. In selected instances the leaves, tender shoots and roots are harvested and used as vegetables. The whole seed of some of the legumes are called *Gram*. Seeds of legumes without seed coat and cotyledons split into half is commonly called as *Pulses* in India. Similarly the split pigeon pea, *Cicer arietinum* L. is referred to as *Dal* in India and Pakistan. According to Vavilov all the main centers of origin of cultivated plants have contributed cultivated legumes of today.

Legumes are rather unique compared to other vegetables in that they can obtain atmospheric nitrogen free through their symbiotic association with the nitrogen fixing bacteria, *Rhizobium* or *Bradyrhizobium* in legumes root nodules. The nitrogen fixed in the

root nodules are not only available to the plant but also they enrich the soil, in varying amounts, when the plants complete their life cycle.

Many leguminous vegetable plants contain toxic substances like trypsin inhibitor (soybean, *Glycine max* (L) Merrill), rotenone (yambean, *Pachyrhizus erosus* L.,) and cyanogenic glucoside (hyacinth bean, *Lab lab niger* L., and *Lathyrus sativus* L.). There are diverse ways by which the toxic effects of these vegetables can be eliminated and they are rendered safe for human consumption.

Depending upon the country some of the legumes are included in the field crops section, others are included in the horticultural crops section, while still others are included in the oilseeds crop section. However, in many of the monographs dealing with vegetable legumes published in different countries almost all these crops are treated as vegetable crops.

In addition to being used as fresh pod, immature seed and mature dry seed, majority of these vegetables are also canned and frozen for the market. Some of the legume seeds are sprouted and they are popular in many Asian countries. Many legumes are also processed and used.

In international trade leguminous vegetables play an important role. Dry seeds, canned and frozen foods and processed food products from leguminous vegetables enter into international market and they are important commodities in foreign exchange consideration both from the point of view of drain and earnings

BOTANY

Legumes are dicotyledonous annuals or perennials. There are about 480 genera and more than 12,000 species in the family *Leguminosae* (commonly called the Pea family). As a group they contain at least 28 different vegetable crops belonging to 18 genera. Almost all the vegetable crops belong to the sub-family *Papilionaceae.*

Leaves of legumes are usually alternate, and mostly compound, pinnate, trifoliolate or digitate. The flowers are perfect (stamens and ovaries occur in the same flower). The flowers have characteristic papilionaceous corolla (Fig. 1). The stamens are arranged in two bundles. Nine stamens are united together to form a bundle or staminal column and one stamen is free. The stamens are commonly referred to as diadelphous. The style is filamentous and ends in a capitate stigma. The flower structure of common bean is shown in Fig. 2. Majority of the legumes are self pollinated. In some cases certain amount of cross pollination also occurs. Bees are the main agents for cross pollination.

When the seeds germinate, in some legumes, the cotyledons remain inside the soil due to limited elongation of the hypocotyl. Such germination is referred to as *hypogeal* germination. Example : Peas, *Pisum sativum* L. In other instances, as in the case of soybean (*Glycine max* L. (Merr.)), and common bean (*Phaseolus vulgaris* L.) the cotyledons are pushed above the soil surface by the rapid elongation and growth of the hypocotyl. Such germination is called *epigeal* germination.

A list of leguminous vegetables commonly grown in South and Southeast Asia are given in Table 2.

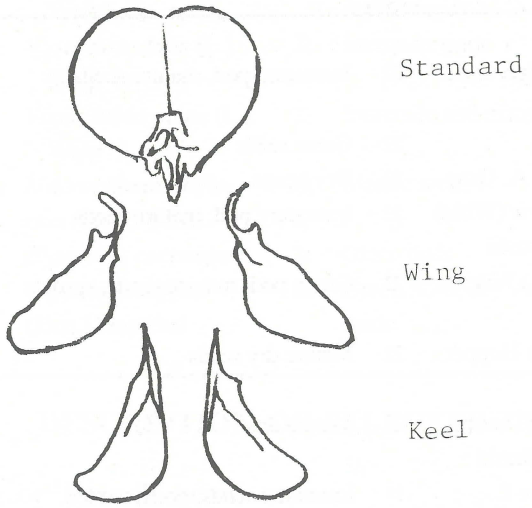

Fig. 1. Typical Papilionaceous corolla

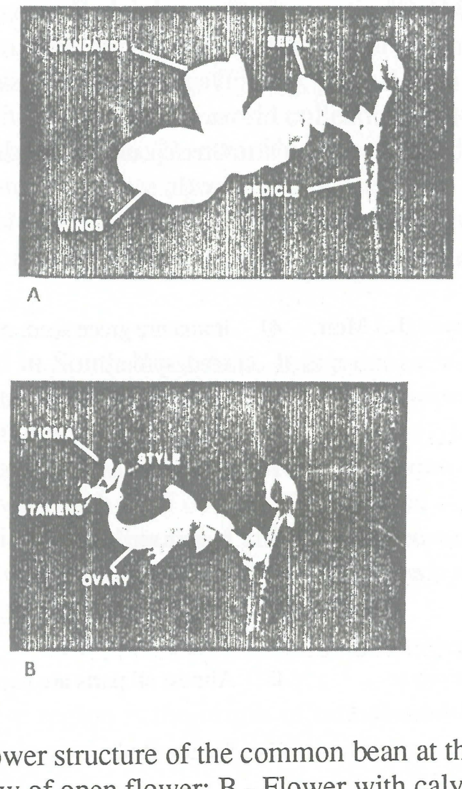

Fig. 2. Flower structure of the common bean at the time of anthesis. A - Side view of open flower; B - Flower with calyx and corolla removed.

Table 2. List of leguminous vegetables.

Crop	Botanical name	Chromosome No.	Edible part	Adapatation
Beans				
Common, Snap, String,	*Phaseolus vulgaris* L.	22	Immature pod, mature seeds	Temp. and Tropic.
Limabean	*P. lunatus* L.	22	Green seeds	Warm season
Tepary bean	*P. acutifolius* A. Gray	22	Dry beans	Dry areas
Adzuki bean	*Vigna angularis* (Willd) Ohwi & Ohashi	22	Immature pod, mature seeds	Warm season
Mungbean, green-gram	*V. radiata* (L.) Wilczek	22	Green pod, mature seeds, sprouts	Warm season
Blackgram, Urd bean	*V. mungo* (L.) Hepper	22	Mature dry seeds	Warm season, dry tropics.
Rice bean	*V. umbellata* (Thunb) Ohwi and Ohashi	22	Mature dry	Warm season
Peas	*Pisum sativum* L.	14	Immature seeds, pods, tender leaves	Cool, humid season
Peanut, Groundnut	*Arachis hypogaea* L.	40	Mature seed, tender shoots and leaves	Tropics and subtropics, warm temp
Swordbean	*Canavalia gladiata* (Jacq.) D. C.	22, 44, 46	Young pods, and beans	Tropics
Pigeon pea, redgram	*Cajanus cajan* L. Mill sp.	22	Young green pods, seeds mature seeds	Warm season
Chickpea, Bengalgram	*Cicer arietinum* L.	16	Green pods, tender shoots, dried seeds	Cool, dry
Clusterbean, guar	*Cyamopsis tetragonoloba* (L.) Taub.	14	Young tender	Dry tropics
Soybean	*Glycine max* (L.) Merr.	40	Immature green seed; mature dry seed, sprouts	Tropics to 52°N
Hyacinth bean, lablab bean	*Lablab purpureus* (L.)	22,	Young pods, tender bean, dried seeds	Dry season
Grass pea, Chickling pea	*Lathyrus sativus* L.	14	Seeds, leaves used as herbs	Cool season
Lentil	*Lens culinaris* Medikus	14	Mature seed	Winter crop
Yam bean	*Pachyrhizus erosus* Urban	22	Succulent roots	Hot, wet tropics perennial
Potato bean	*P. tuberosus* spreng	22	Tubers	Perennial
Winged bean,	*Psophocarpus tetragonolobus* D. C.	18	Almost all parts are used	Tropical Asia
Fenugreek	*Trigonella foenum-graecum* L.	?	Mature seeds	Winter

Faba bean, broad bean, Horse bean, Windsor bean	*Vicia* faba L.	12	Green beans, dry seeds	Temp. Cool season
Cowpea, Catjang	*Vigna unguiculata* (L.) Walp	22	Immature pods, young shoots dry beans	Trop. Africa
Yardlong bean, Asparagus bean	*V. sesquipedalis* (L.) Walp	22	Immature pods	Warm season
Bambara groundnut	*Vigna subterranea* (L.) Walp	22	Immature and mature seeds	Tropical Africa
Horsegram	*Macrotyloma uniflorum* (Lam.) Verdc	20, 22	Mature seeds	Dry tropics
Runner bean	*Phaseolus coccineus* L.	22	Green pods	Temperate
Moth bean	*Vigna aconitifolia* (Jacq.) Marechal	22	Green pods, dry whole or split seeds	Tropical

DESCRIPTION OF SELECTED LEGUMES

1. Snap, String or French bean

Phaseolus vulgaris likely originated from Central America. It is commonly associated with corn and squash culture in the tropical Latin American countries.

It is an annual, twining vine or bush with alternate trifoliolate leaves (Fig. 3). Indeterminate cultivars are 2-3m tall while the determinate cultivars are 20-60cm tall. Stem angular or nearly cylindrical; Inflorescence axillary or terminal racemes, with white, pink, lilac or purple flowers; stamens diadelphous (9+1); ovary laterally compressed with 4-12 (usually 7) ovules; style upturned and spiralled with collar of fine hair below the stigma. Stigma ellipsoid, glandular, directed adaxially (Fig. 2); germination is epigeal.

CIAT in Cali, Colombia has classified the world collection into following four main types by growth habit : 1). dwarf determinate, 2). dwarf indeterminate,3). prostrate indeterminate and 4). climbing indeterminate. Beans are also classified according to use as follows : snap or string beans (for tender fresh pods); green shell beans (green shelled condition, normally bush and climbing varieties); and dry-shell or field beans (mature dry seeds);

2. Peas

Peas probably originated in South-West Asia. It is a cool season crop in the subtropics and also grown at higher altitudes in the tropics.

Botanically it is an annual climbing herbaceous plant (Fig. 4); leaves are pinnate with 2-3 pairs of leaflets and a terminal tendril, at base with 2 leaf-like stipules. Flowers are axillary racemes with 1-2 flowers; ovary with 4-15 ovules. Germination is hypogeal. It is a long day plant. The flowers are strictly self-pollinated. Classification primarily by the type of seeds, either round or wrinkled. Round seeds are for fresh green peas or mature dry seed while wrinkled are used for canning or freezing while it is immature.

3. Mungbean

India or the Indo-Burmese region is the origin of mungbean. In South-Asia it is one of the major leguminous vegetable crop. In South-East Asia it is one of the three main legumes.

It is an erect or semi erect annual (Fig.5); true trifoliolate leaves are alternate and the leaflets are ovate or deltoid. Flowers are large and the inflorescence is axillary racemes. Pods spreading, pendent, cylindrical, straight, pubescent or glabrous. Seeds are green or yellow, occasionally brown or blackish, with dull or glossy lustre. Germination is epigeal.

4. Vegetable Soybean (*Edamame*)

Soybean originated as a demesticate in the eastern half of northern China around the 11th century BC. Soybeans were introduced from China to USA, Japan, Korea and South and South-East Asian countries at different times.

Usually an erect, bushy, annual, herbaceous plant (Fig. 6), leaves are alternate, trifoliolate, glabrous to pubescent; leaflets ovate to lanceolate, entire, base rounded, apex acute to obtuse; inflorescence axillary or terminal racemes with 3-30 flowers; flowers small, purple or white; stamen 10, diadelphous, style curved with capitate stigma; pods dehiscent; seeds usually globose, yellow, green, brown, black or mottled; germination is epigeal. Large yellow or green seeded varieties with gray hilum color is preferred for use as vegetable soybeans. Based on latitudinal adaptation soybean cultivars in the U.S.A. and Canada have been classified into 13 maturity groups (MG). The MG 000, 00, and 0 are early and adapted to extreme North latitudes while MG IX and X are late and adapted to tropical latitudes. However, this MG system breaks down in the tropical and subtropical latitudes.

Fig. 3. *Phaseolus vulgaris* L. 1 - fruiting branch; 2 - inflorescence; 3 - seeds.

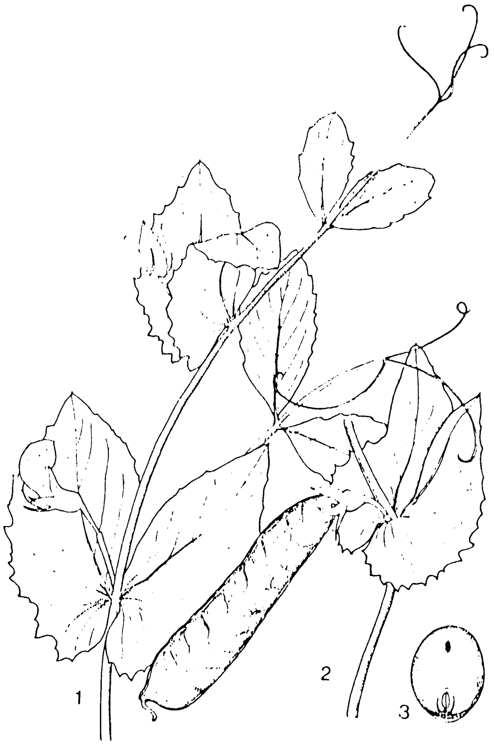

Fig. 4. *Pisum sativum* L. 1 - branch with flower; 2 - branch with fruit; 3 - seeds.

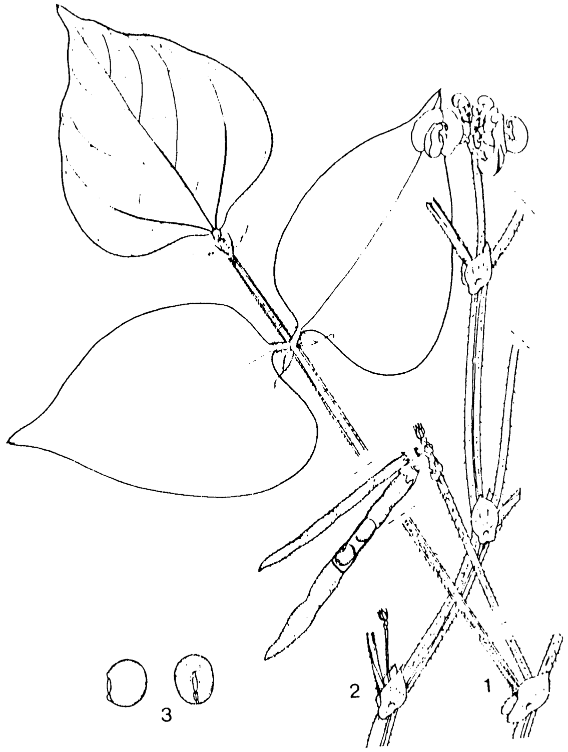

Fig. 5. *Vigna radiata* (L.) Wilczek. 1 - fruiting branch; 2 - flowering branch; 3 - seeds.

Fig. 6. *Glycine max* (L.) Merr. 1 - flowering branch; 2 - fruiting branch; 3 - seeds.

CONTROLLED HYBRIDIZATION PROCEDURES

1. Snap bean

Artificial hybridization of field-grown plants are largely unsuccessful. Majority of the hybridizations are done in plants grown in greenhouses or in protected conditions. *P. vulgaris* is a short day plant. Snap bean is highly self-pollinated and it can be safely assumed that no outcrossing occurs in greenhouse grown plants.

Pollen grain dehiscence and self-pollination occur in the late bud stage, usually at night, with pollen tube growth commencing almost immediately.

Fine tipped, curved or straight, forceps a small bottle of alcohol for rinsing the forceps, cellophane tape and dispenser, small tags on strings, coin envelopes about 65 x 110 mm and a magnifying lens are the tools needed for pollination.

The stigma is receptive at least 2 days prior to and 1 day after anthesis. Plump buds, with color, will open the following day, are chosen as female parent. Already self-pollinated stigma is swollen, dried and light green in color. Before pollination stigma is white and sticky.

Emasculation and cross pollination can be done throughout the day. Cross pollination can be made either with or without emasculation. The standard petal is opened by inserting the forceps into the suture and pushing from side to side. Next the winged petals are removed. The coiled keel petal must be removed to expose the anthers . Make a small incision on the top of the keels and grasp the upper lip and peel it up and back. Once when the keels are

removed stigma and anthers are exposed. Often the keel breaks and it is necessary to remove enough of the keel. Then remove the 10 stamens without rupturing the anther sacs. Make sure to count the stamens removed. Dip the forceps in alcohol periodically to prevent contamination.

Crosses made prior to 11:00 hrs and after 15:30 hrs are more successful than other times. Pollinations are made either by rubbing the pollinated stigma or by hooking on to the stigma of the emasculated female parent. In the hooking method the pollinated stigma of the male parent is removed from the male and rubbed against the female stigma and left in the female flower by hooking it through the style of the latter near the stigmatic surface. Clamping method is used without emasculation. Pollen laden stigma of the male is hooked behind the protruding stigma of the female.

To prevent desiccation of freshly pollinated stigma, the standard petal is closed gently following pollination and bud may be enclosed with cellophane tape. After pollination, place a tag around the pedical of the female flower.

A success rate of 30 to 40% is common with rubbing method. The success rate with hooking method is 70 to 90%.

2. Peas

A pair of forceps with sharp tips, 95% ethanol for killing undesired pollen, tags to identify crosses and a pencil to record the cross on the tag are the only equipments needed for artificial hybridization.

Strong, vigorously growing young plants which began to flower offer the best for successful artificial hybridization. Success rate with older plants are very poor. Cooler times with high relative humidity occurring during morning is preferrable for field hybridization. In the greenhouse and in controlled growth cabinets hybridization can be done throughout the day. Pea flowers are large and easy to handle for hybridization (Fig. 7 A4). The flower bud for crossing will have petals extending beyond the sepals (Fig. 7 A2) in which anthers are yet to dehisce. Younger flower buds are more difficult to emasculate and are easily damaged (Fig 7 A1) and may set a fewer seeds. Remove all flowers other than the ones to be emasculated and pollinated from that peduncle to reduce competition for nutrients.

In emasculation the flower the first step is to carefully tear away the tip of the sepal with the forceps from in front of the keel. By moving the standard petal back and the wings sideways insert the sharp tip of the forceps and slit the keel (Fig. 7B). Spread the keel apart and held them down with finger and thumb. Remove the 10 anthers by grasping the filament with the forceps and carefully pulling (Fig. 7C). Count the anthers to make sure that all 10 anthers have been removed.

An alternative emasculation procedure is to roll the standard and wing petals back and hold them with thumb and index finger. Then grasp the keel and tear off its upper part along with the anthers. If the single free anther remains, it is removed with the finger nail or point of forceps or pencil.

Pollen can be collected at any time of the day from freshly dehisced anthers. Pollen dehiscence occurs when the petals begin to open. Good pollen will be rich moist yellow. Untreated pollen could be stored for 6 days after dehiscence and still useful for fertilization. Vacuum drying and storage at 25°C extended pollen viability for 1 year. Use a tooth pick, tip of the forceps, a cotton swab, or a stigma to collect and transfer the heavy sticky pollen (Fig. 7D). The receptive surface is the elliptical stigmatic tip of the sytle, not the hairs on the

concave side. Tag the pollinated flower to identify the cross (Fig. 7E). Identify the male and female parents, date of pollination and name of the pollinator. Use a water proof pen.

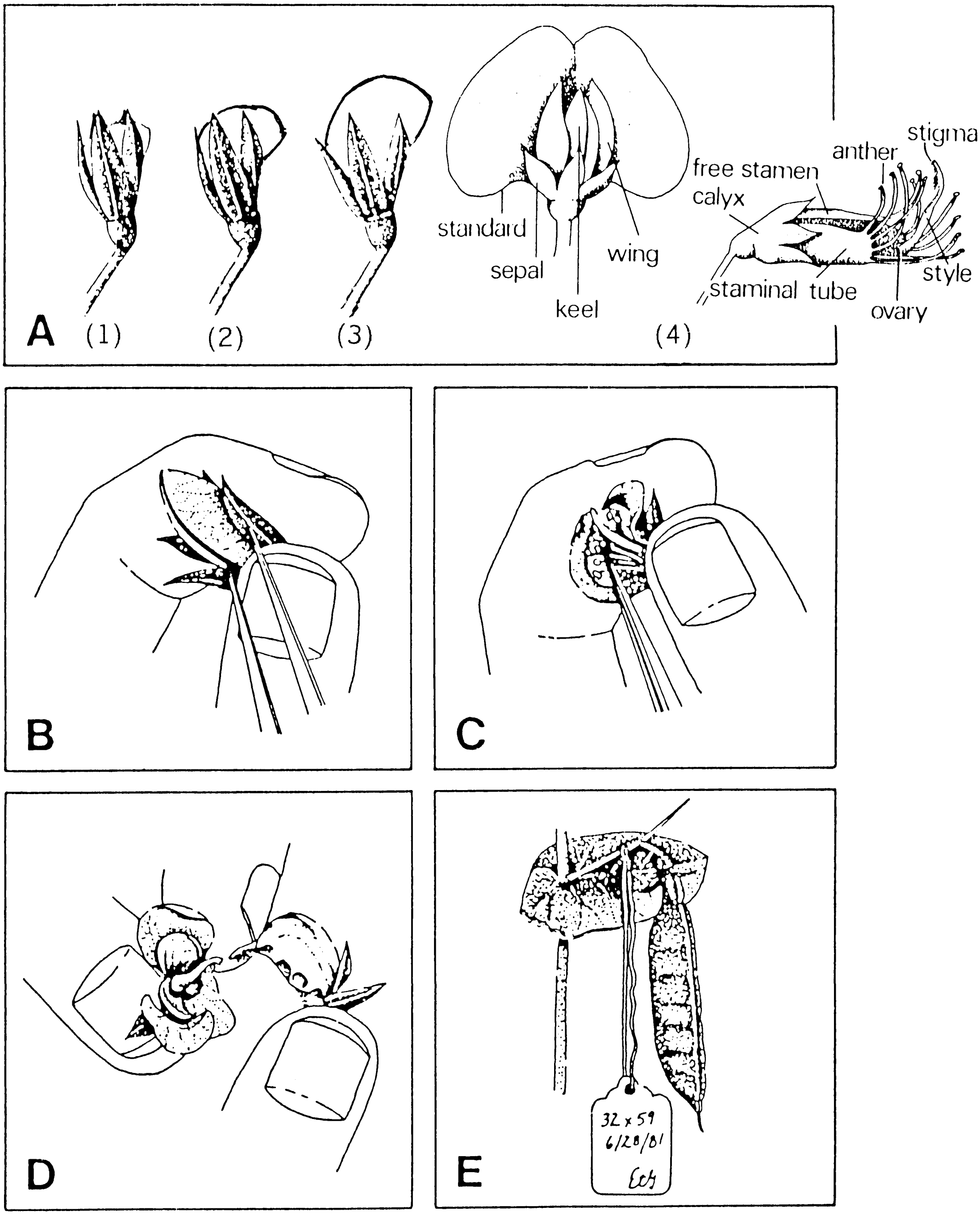

Fig. 7. Pea flower - Stages in pollination. A1 - not ready for pollination; A2 - just ready for pollination; A3 - already pollinated; A4 - open flower; B - opening the keel; C - removing anthers; D - using pollen laden style to transfer pollen to emasculated flower; E - developing pod with tag.

for several weeks in a desiccator at 3°C. Pollinated flowers are identified with tags as described for other crops. An experienced breeder can hybridize 20 to 50 flowers per hour in indeterminate and determinate cultivars respectively with a success rate of 50%. Steps in emasculation and pollination are shown in Fig. 8.

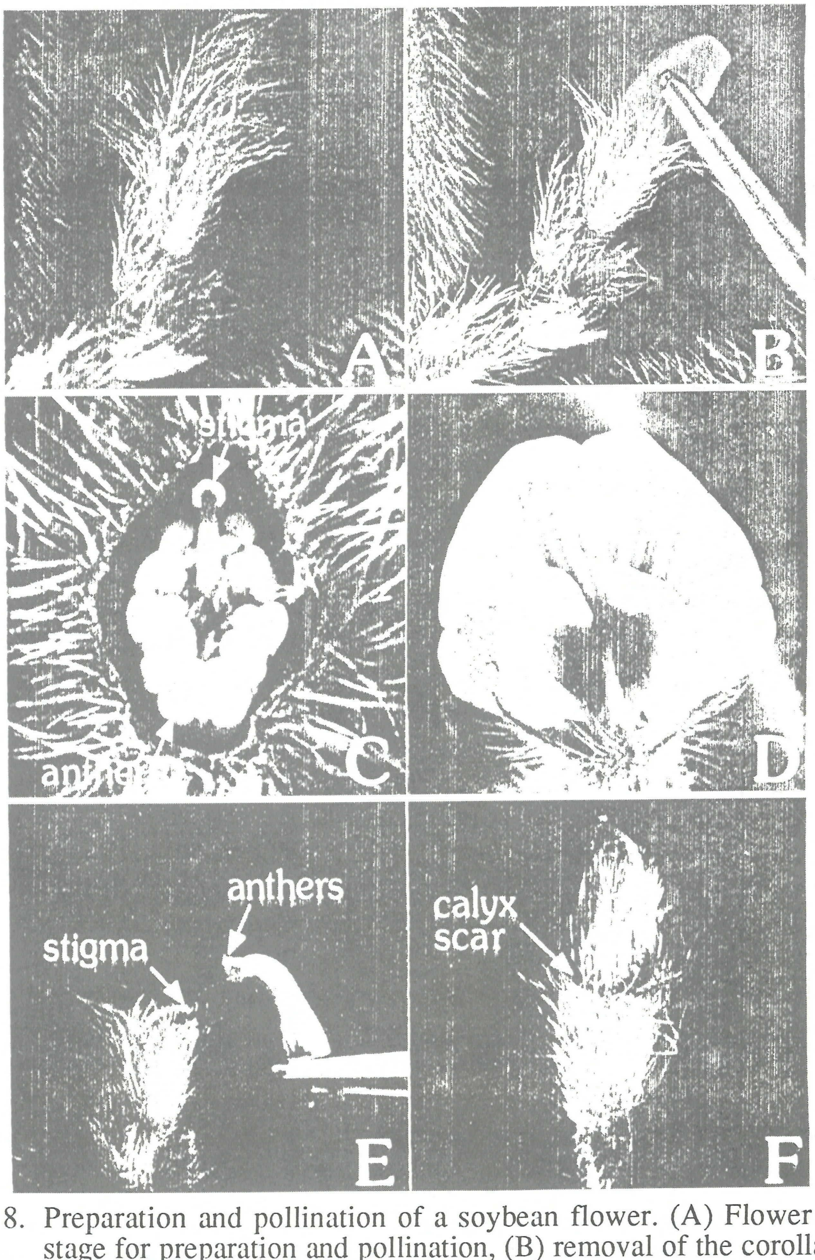

Fig. 8. Preparation and pollination of a soybean flower. (A) Flower at the stage for preparation and pollination, (B) removal of the corolla from the female flower after the calyx has been removed, (C) ring of 10 anthers and the stigma, (D) flower with pollen available, (E) pollination of the stigma, and (F) a pod 7 days after pollination with the calyx scar differentiating it from self-pollinated pods. (Photographs A, B, D, E, and F by C. J. Deutsch and P. A. Krumhardt, Iowa State Univ., Ames, Iowa; photograph C by G. L. Berkdy, Ohio Agric. Res. and Devel. Ctr., Wooster, Ohio).

3. Mungbean

Self pollination of mungbean flowers begins from 21:00 - 22:00 hours and completed around midnight. The following morning flowers begin to open and remain in full bloom until shortly before noon. By mid to late afternoon flowers are fully closed. Cleistogamy is common. Self-pollination is the rule. However, usually 0.4% cross pollination by bees have been reported. At AVRDC upto 13% natural cross pollination was observed in some genotypes.

For emasculation, the standard petal is pushed to one side and the wing petal outward with a dissecting needle. The keel petal and anthers are removed with forceps avoiding injury to the stigma. From the male parent a stigma is selected that is covered with fresh pollen from dehisced anthers and the pollen laden stigma is brushed across the stigma of the emasculated flower.The wing and standard petals are returned into place after pollination. Emasculation in the evening and pollination in the following morning gives maximum seed set. Success rate varies from 20% to 60% pod set.

Recently a new technique has been developed. The tip of the bud is opened with fine tipped forceps to expose the style and stigma, and the anthers are slowly dislodged from the filaments. After pollinating the emasculated bud, a cellaphane tag is placed over the opening to seal the bud. Using this method emasculation and pollination can be done in one minute. The success rate is 60%.

4. Vegetable Soybean

The soybean is a short day plant. Genetic variability for sensitivity to photoperiod exists. Temperatures below 21°C and above 32°C can inhibit floral initiation and seed set. Artificial hybridization is most successful between 26°C and 32°C. High humidity improves the success of artificial hybridization. Success with growth chamber or greenhouse hybridizations are limited in some cultivars (especially in temperate countries).

Soybean flowers are self pollinated on the day when petals open. Natural outcrossing through honeybees is about 1%. The stigma is receptive a day prior to and 2 days following anthesis. Prior to anthesis the anthers are below the stigma. As anthesis approaches the filaments elongate rapidly and surround the stigma. The anthers dehisce on the day of anthesis. Within 10 hours after the pollen grains fall on the stigma the pollen tubes reach the ovary and fertilization is effected.

The equipment needed are a pair of forceps with fine tips and a smooth interior surface. Plastic or paper tags to identify the pollinated flowers. A 2.5x magnifiers mounted on a headband is useful to see the flower parts clearly. Petri dishes or paper envelopes are used to collect male flowers. Desiccators with calcium chloride crystals are used to dry male flower and obtain adequate pollen in some environments.

The buds with corolla just visible are chosen for emasculation. Generally for each node no more than two buds are chosen for pollination. All other flowers are removed. First the five calyx are removed with the forceps. By grasping just above the calyx scar all the petals can be removed by gently lifting and wiggling movements. Sometimes one can remove all the anthers along with the petals. Otherwise remove all 10 stamens by counting them.

Emasculation is unnecessary if proper bud is chosen for pollination. But emasculation is recommended. Anthers are difficult to remove if the flower is immature. If the stigma is surrounded by the anthers then pollination has already occurred.

The female flower after emasculation is immediately pollinated by taking the stamens from the male plant and smearing on the stigma of the female flower. Flowers can be stored

GENERAL PRINCIPLES OF BREEDING SELF POLLINATED CROPS

The major goal of any plant breeder is to develop improved varieties that is profitable to the farmers and acceptable to the consumers and processors.

Populations developed from a single genotype or a mixture of genotypes are commonly referred to as strains, experimental strains, or breeding lines. Plant breeder evaluates thousands of strains every year. True to type and identity are essential qualifications of a variety (also called cultivar). In self-fertilized crop plants, since the individuals in a population tend to be homozygous, the range of purity within a variety depends upon its origin and genetic stability. When a variety is developed from a single genotype which is true breeding, in a self fertilized crop, they are called pure line.

In a crop which is predominantly self-pollinated the plants in the population will be largely homozygous. This assumption is due to the face, a). gene pairs that are homozygous (AA or aa) will stay as homozygous with selfing, b). gene pairs heterozygous will segregate to produce equal proportions of homozygous and heterozygous progeny.

By selfing heterozygosity is reduced by one-half with each successive selfing (Table 3). As can be seen from Table 3 with each generation of selfing the proportion of heterozygous individuals decreases while that proportion of homozygous true breeding individual increases. It requires about five to eight generations of selfing to reach an acceptable practical level of homozygosity. At such stage, homozygous individuals are isolated and multiplied to produce a pure line population. Variability in pure lines may arise due to natural cross pollination or mutation. However, the progenies of such variants again quickly segregate giving rise to homozygous genotype.

Table 3. In a self pollinated crop the proportion of heterozygous individuals decreases and homozygous individuals increases with each successive generation of selfing.

Generation	Percentage of		
	Homozygous dominant	Heterozygous	Homozygous recessive
F_1	0	100	0
F_2	25	50	25
F_3	37.5	25	37.5
F_4	43.75	12.5	43.75
F_5	46.875	6.25	46.875
F_6	48.4375	3.125	48.4375
F_7	49.21875	1.5625	49.21875

1. Breeding methods

The common methods that are widely used are (a). introduction, (b). selection and (c). hybridization and selection. Direct introduction of promising varieties that are pure is the first step. In cases when there is a mixture in an introduced variety or locally available varieties then selection and pureline development is practiced. But when desirable characters are distributed in different varieties which need to be combined then hybridization and selection is

resorted to. In breeding self pollinated crops, enclosing flowers in bags to ensure selfing as in cross pollinated crops is unnecessary.

Two methods of selection are practiced in breeding self pollinated crops. They are (a). mass selection and (b). single plant or pureline selection.

A. Mass Selection

Selection of phenotypically similar plants and compositing the seeds without progeny testing is called mass selection. Plants of the population may not necessarily be homozygous. Therefore, phenotypic selection may be necessary in subsequent generation if purity is desired. However, the genetic variation within a mass selected population may offer some buffering against differing environmental variation.

B. Pureline or Single-Plant Selection

The progeny of a single homozygous self-pollinated genotype is called a pureline. It is more uniform than mass selected line. It is assumed that the selected genotype is homozygous for all gene loci which is invariably not true. New genotype are not created by pureline. Purelines may become impure due to a). mechanical mixtures with others, b). natural outcrossing and c). mutations.

C. Hybridization and Selection

In self-pollinated crops the following three major methods of selection in segregation population are practiced following hybridization : a). pedigree selection, b). bulk population and c). single seed descent.

In pedigree method desirable single plants are selected in the F_2 generation. The progenies of selected plant are further reselected until genetic purity is obained (Fig. 9). In bulk-population method selection is delayed until F_5 or F_6 when practical homozygosity has reached. When F_2 plants and their progenies are advanced in succeeding generations by single seeds until genetic purity is obtained, then it is called single seed descent method (Fig. 10).

A number of modifications of pedigree and bulk methods are used by different plant breeders. A combination of the two methods are also attempted. In addition, recurrent selection procedure is also used in recent years. A group of elite parents are chosen. They are intermated. The progeny of the intermated population is harvested individually and evaluated in a replicated test. The best lines are selected and intermated for second cycle of testing.

Instead of testing and selecting at later generations, when the genotypes are fairly homozygous, early generation testing is also practiced with varying levels of success in different crops.

In recent years the objective in hybridization is to create as much variability as possible in the source population to increase the combination of favourable alleles specifically for quantitative traits and ensure maximum gene recombination. It is also directed to break the tight linkage blocks.

Back crosses are used to transfer some qualitatively inherited characters from a genotype to a popular cultivar. Modified backcrosses involve the use of more than one recurrent parent.

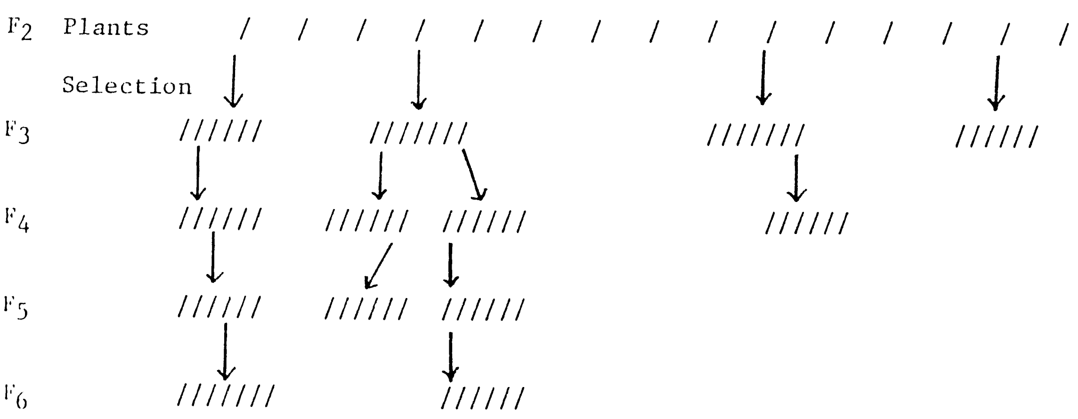

Fig. 9. <u>Pedigree method</u>. Best rows and best plants are selected in each generation.

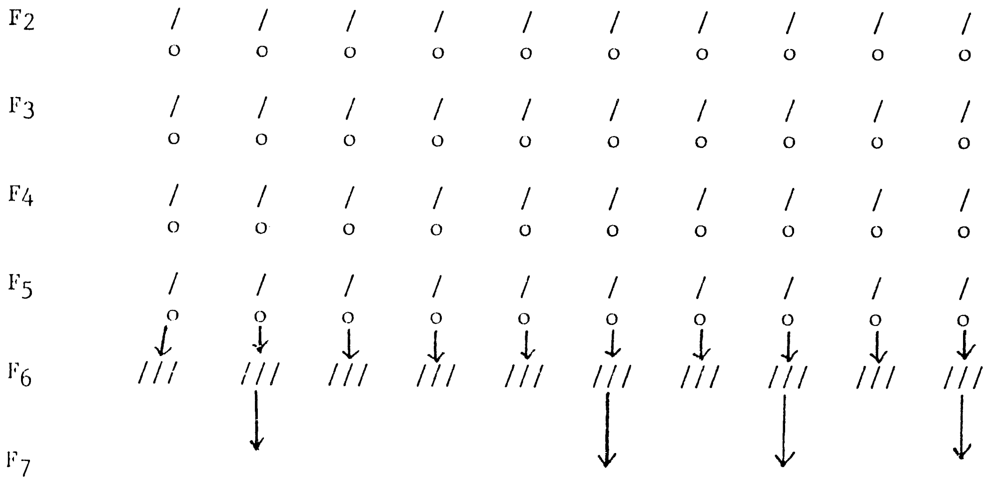

Fig. 10. <u>SSD method</u>. One seed is harvested from each F_2 plant and advanced; in F_3 again one seed is harvested and advanced. It is continued until F_5. Then select best family.

BREEDING OBJECTIVES FOR SPECIFIC CROPS

1. Snap bean

Collection of germplasm to enrich the genetic diversity, and an understanding of the inheritance of the available genetic diversity are two non-specific breeding objectives. The germplasm committee of the Bean Improvement Cooperative has compiled a bean gene catalog.

The objectives of the bean breeding program should take into consideration the farmer, the seedsman, the processer and the consumer. Good seed quality, concentrated pod maturity, strong upright narrow growth habit, resistance to various disease and insects, tolerance to environmental stresses are some of the most important objectives.

In areas or seasons with high rainfall pole types are preferred. In other seasons there is an interest in developing bush types. As in other crops high yield is one of the important objectives. Fresh market quality and sloughing free cultivars for canning industry; and short periods for whole pod processing are other important objectives.

2. Peas

The major breeding objectives are yield, improvement of standing capacity of the crop, regional adaptability, suitable plant type, lodging and shattering resistance, disease and insect resistance, environmental stress resistance and quality for different purposes.

Specific varieties are developed with round and wrinkled seeds; fresh edible pods; shelling green peas for fresh market or for canning and freezing; for mature seed and for tender shoots (specifically in Taiwan).

In the case of edible podded peas elimination of strings from the pods, dwarf vine bearing double pods, thick crisp pod wall and resistant to prevalent diseases such as root rot, powdery mildew and virus diseases are the major objectives.

Development of altered foliage types, as shown in Fig. 11 especially semi-leafless tendril types is gaining interest since they have the advantage of improved standing ability, color uniformity of berry, and pest control.

3. Mungbean

Mungbean is a very short duration crop. The current goal of the program is to develop stable, high yielding mungbean lines with resistance to diseases and pests, synchronized maturity and improved quality suitable for the tropics and subtropics. The specific objectives vary from country to country. Some of the common objectives are as follows :

a. to develop stable high yielding (> 2.0 t/ha), early and uniformly maturing, large seeded cultivars;
b. to incorporate reduced sensitivity to photoperiod and temperature variation;
c. to add resistance to Cercospora leaf spot (CLS), powdery mildew (PM), viruses, beanfly, bruchids and pod borer;
d. to develop tolerance to lodging, seed shattering, field weathering, drought and other environmental stresses;

Some countries prefer dull seed coat (e.g. Taiwan, Korea) while others prefer shiny seed coat (India, Pakistan). Most countries prefer large seeded types while Korea prefers small seeded varieties. In the Philippines yellow seeded varieties are also preferred over green seed in some regions.

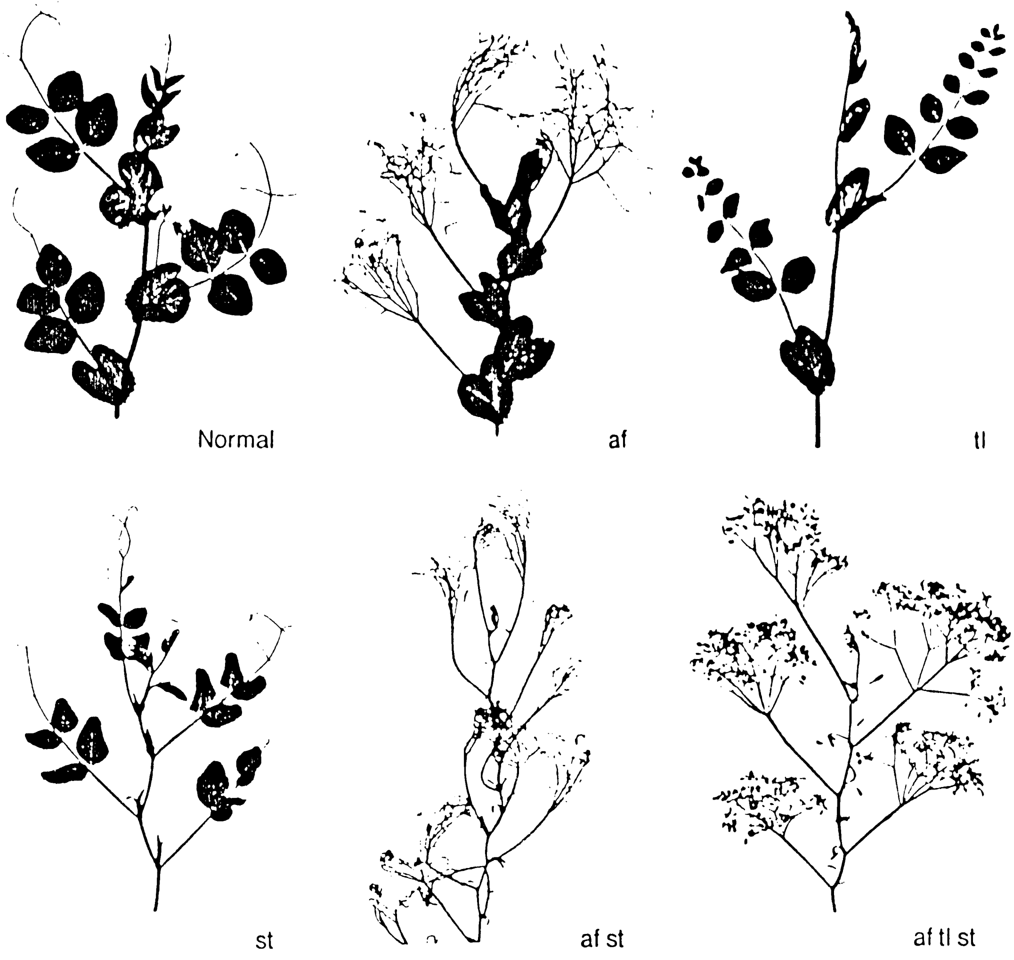

Fig. 11. Some pea foliage types. Normal has the genotype *Af /Af, Tl /Tl, St /St*. The homozygous recessive gene(s) responsible for each different type is (are) shown below each type.

4. Vegetable Soybean

There is no universally accepted definition of vegetable soybeans. In general, the taste, flavor and seed size are the primary consideration for vegetable soybean. In breeding vegetable soybeans for the Japanese market the pods and seeds should be large (the dry weight of 100 seeds should be 30 g or more; and 500 g packet of frozen pods should contain 175 pods or less); pods should have two or more seeds; one seeded, malformed, yellow, or damaged pods are unacceptable; the pod and seed color should be bright green; gray pubescence on the pod and light brown or gray hilum is required; good flavor and texture are needed; slightly sweet taste is preferrable while oily taste is undesirable; short cooking time is desired; when once the crop reaches the maturity stage that is right for harvesting the time taken to reach the next growth stage (yellowing of pods) should be longer (good 'holding capacity'). Pods should preferrably remain green for a longer period under high temperature after reaching the harvest stage to enable the processers to harvest in phased stages.

SELECTION TECHNIQUES AND EVALUATION

1. Snap Bean

In selecting for strong upright plant, commonly referred as "Tender crop plant type" "weak kneed types" should be discarded.

PI 165426 has small leaf size and was reported to have resistance to rhizoctonia root rot and root-knot nematode and was the base for the development of several bush type cultivars.

For a review of breeding for disease resistance see the references by Schwartz and Galvez (1980); Silbernagel and Zaumeyer (1973); and Zaumeyer and Meiners (1975). Note that these references can be located in the reference by Silbernagel (1986).

Some of the recently identified sources of resistance to major diseases are listed in Table 4.

Table 4. Sources of resistance to diseases.

Disease	Pathogen	Resistant sources	Mechanism (Genes)
Bean Common Mosaic Virus	BCMV	Most US snap beans	I resistance : bc-1^2, bc-2^2, bc-3
Curly top	virus	Apollo, Blue Mountain, Gold Crop, Wonder Green	Epistatic dominant
Rust	*Uromyces Phaseoli* (Ruben) Wint.	PR-190, 8BP-3, Resisto BPSR-130	
Anthracnose	*Colletotrichum* sp.	8BP-3	ARE
Root rots	*Fusarium solani*	—	Quantitative
	Pythium	RRR-36,RRR-46	
	Aphanomyces euteiches f. sp. *phaseoli* Phend & Hag	RRR-36, RRR-46	
Halo blight	*Pseudomonas syringae* pv *Phaseolicola* (Burk) Comb. nov.	Noorinbee, RH-13 Nebraska, HB-76-1	

Since there are several market preferences for which beans are produced, specific characters that are acceptable to all needs are unavailable for use as selection criteria.

Initial emphasis in early generation should be screening for resistance to locally prevailing diseases. The remnant from the segregating population should be evaluated for horticultural and agronomic characteristics using the data sheet (Table 5). Since the diseases and pod characteristics may vary widely between locations and seasons it is essential to screen and evaluate the segregating population in different seasons and different production locations. The undesirable types and susceptible plants should be ruthlessly discarded.

Simply inherited traits could be recovered and stabilised at F_2 or F_3 generation itself. Selection for more complex quantitatively inherited characters with low heritability should be postponed to F_5-F_8 generations. During early generations for such quantitative traits, such as root rot resistance low selection pressure should be applied and highly sensitive individuals can be discarded.

Table 5. Snap bean data sheet.

Name ______________	Snap Bean Cultivar Trial	Date Sown ______________
Institute ______________	Data Sheet	Expt. Site ______________
Address ______________		(Elevation) (______________)

Plot No.	Entry	Rep. No.	Total Stand	Harvest sequence							MPN	MPY (g)	TY (t/ha)	MY (t/ha)	PL			PW			Diseases/pests		Remarks
					1st	2nd	3rd	4th	5th	Total					1	2	Ave.	1	2	Ave.	Rust	Insect damage	
				DH																			
				PN																			
				TPW(g)																			
				MPW(g)																			
				DH																			
				PN																			
				TPW(g)																			
				MPW(g)																			
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				DH																			
				PN																			
				TPW(g)																			
				MPW(g)																			

DH=Date harvested; PN=No. of pods harvested; TPW=Weight of pods harvested; MPW=Weight of marketable pods after removing defected pods;

MPN=Mean pod no. per plant=Total PN/Total stand; MPY=Mean pod yield per plant=Total TPW / Total stand; TY=Total yield= $\frac{\text{Total TPW(g)}}{\text{Plot size (m}^2\text{) X 100}}$;

MY=Marketable yield= $\frac{\text{Total TPW(g)}}{\text{Plot size (m}^2\text{) X 100}}$; PL and PW=Pod length and pod width, respectively. Measure length and width of randomly chosen ten pods at optimum harvest and take their mean; Diseases/pests damage : Score the severety with scales 0=no damage to 9=most serious damage.

Screening for virus resistance is done both in the field and in the greenhouse. Segregating population is kept at 24-48 hr in the dark prior to mechanical inoculation. At 24°-28°C virus symptoms are expressed in 10-14 days. Symptomless plants should be inoculated again regardless whether it is in the field or greenhouse to confirm the resistance.

Similar screening techniques are available for bacterial and fungal diseases.

For root rot a rating index has been developed. The disease index is calculated as follows

$$\frac{100[0(\text{No. at } 0) + 1(\text{No. at } 1) + 2(\text{No. at } 2) + 3(\text{No. at } 3) + 4(\text{No. at } 4) + 5(\text{No. at } 5)]}{(\text{Total plants}) \times (\text{No. of disease categories} - 1)}$$

where, the sum of the products (number of plants in each disease category) x (numerical value of that category) is multiplied by 100. That product is divided by the product of the total number of plants times one less than the number of disease categories used. This system allows for comparisons among researchers who use different disease severity ratings (e.g. 0-4, 1-5, 1-9) by putting all results on a 0 to 100 basis.

What to Save? Category 0 is immune, 1 is highly resistant, 2 is moderately resistant, 3 is moderately susceptible, 4 is very susceptible, and 5 is highly susceptible. Plants with a rating of 0 or 1 are usually considered resistant enough to save for seed production.

A schematic representation of breeding procedure is given in Fig. 12.

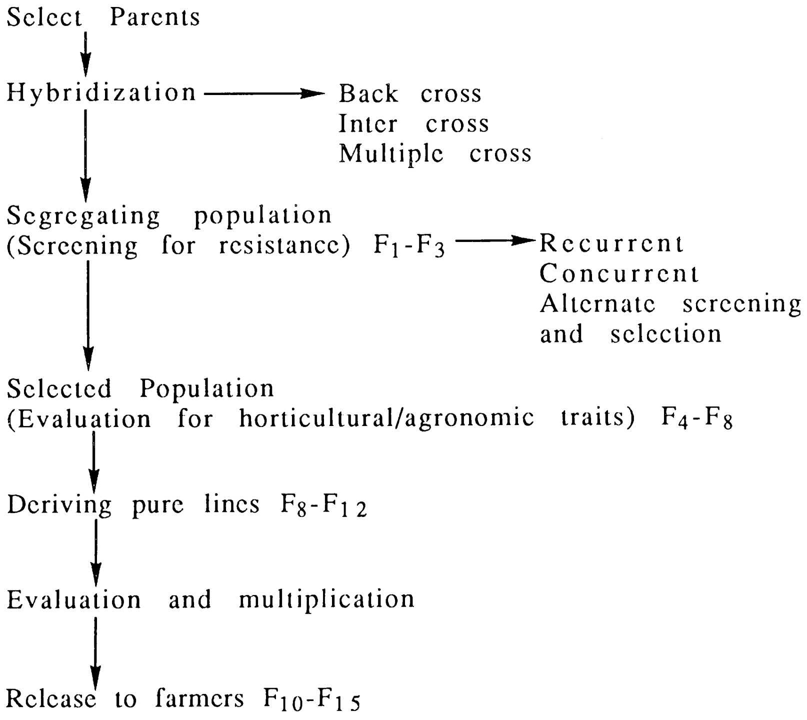

Fig. 12. Flow chart of bean breeding program.

Normally it takes about 9 to 10 years to develop a new improved variety. For yield evaluation 3 to 6m long single row plot with 3 to 6 replications are used. Sequential planting and different harvest dates are used for evaluation. At least two season data are needed to promote the lines for extensive testing. A processed quality evaluation form is given in Fig. 13.

Variety | Sieve Size | Date Harvested ___________

Location | Canned-frozen Sample | Date Evaluated ___________

Style Pack : Whole Cut

Quality Evaluation :

Appearance :	Attractive	5	4	3	2	1	Poor
Liquor :	Clear	5	4	3	2	1	Discolored
Pod Color :	Green	5	4	3	2	1	Gray
Suture Color :	Green	5	4	3	2	1	Brown
Defects :	Low	5	4	3	2	1	High
Flavor :	Good	5	4	3	2	1	Poor
Texture:	Firm	5	4	3	2	1	Mushy
String :	No String	5	4	3	2	1	Stringy
Sloughing :	None	5	4	3	2	1	Excessive
Carpels :	No Slippage	5	4	3	2	1	Excessive

Quality Rating. Total [ ]

Comments :

10 seed length	m m	
Seed Range	min-max	
Deseeded Pods Wgt.	0.00g	
Seed Wgt.	0.00g	
% Seed		Seed Grade
Fiber Basket #		
After Drying Wgt.	0.0000g	
Before Drying Wgt.	0.0000g	
% Fiber-Blender Method	(diff in g)	
Fiber Grade		

Fig. 13. Processed quality evaluation form.

Yield, maturity and sieve size data are useless unless they are related to quality. The quality traits include flavor, texture, carpel separation, skin sloughing, interlocular cavitation, internal tissue breakdown and color.

2. Peas

Peas are one of the first crops studied by Gregor Johann Mendel who proposed the genetic basis of heredity. Extensive genetic studies have unravelled the inheritance of most of the qualitative characters, their linkage relationships and the chromosome association. A genetic map has also been prepared.

Round seed is dominant over wrinkled (gene R) and it is easy to select. All garden, canning or freezing cultivars carry green cotyledons (gene i). It is usually necessary to chip away a portion of the seed coat to expose the cotyledon when scoring for cotyledon color.

Greenhouse or field disease nurseries are established to screen for common root rot caused by *A. euteiches*. Roots of seedlings are inoculated with a mycelial - zoospore suspension of the fungus. The seedlings are then replanted in growth medium and held at about 25°C. Two weeks after inoculation the lines are rated.

Screening for different races of *Fusarium* is usually done in the greenhouse. Resistance to powdery mildew screening is done in the field.

Virus disease resistance screening is done by artificially inoculating the plants.

The pedigree method and a combination of bulk or pedigree and SSD methods are used by judiciously planting inbreeding generations in the greenhouse and field in the three different generations (Table 6).

Table 6. Pedigree-Bulk or Pedigree-Single-Seed Descent Breeding Scheme.

Operation	Location	Season
Make cross	Greenhouse	Fall
Grow F_1 plants	Greenhouse	Spring
Grow F_2 plants and select desired types	Field	Summer
Grow F_3 plants to advance generations	Greenhouse	Fall
Grow F_4 plants to advance generations	Greenhouse	Spring
Grow F_5 plants and select desired types	Field	Summer
Disease test F_6 plants	Greenhouse	Fall
Increase seed of desired F_6 plants	Greenhouse	Spring
Grow single-plant selections on trellises	Field	Summer

A method used to transfer a recessive gene for disease resistance to a successful cultivar is shown in Fig. 14.

3. Mungbean

Pedigree selection is commonly practiced in segregating generations following hybridization. Most mungbean cultivars have been developed from two parent crosses. For example, 'PAGASA' 1 is from the cross "CES 87" x 'ML-5; "VC 1560 Sel. A" is derived from a three parent cross 'BPI Glabrous 3' x ('CES 44' x 'ML-3').

A "plant type" concept was proposed that focussed on short, compact plants; high harvest-index; reduced photoperiod sensitivity, early maturity and more determinate growth habit.

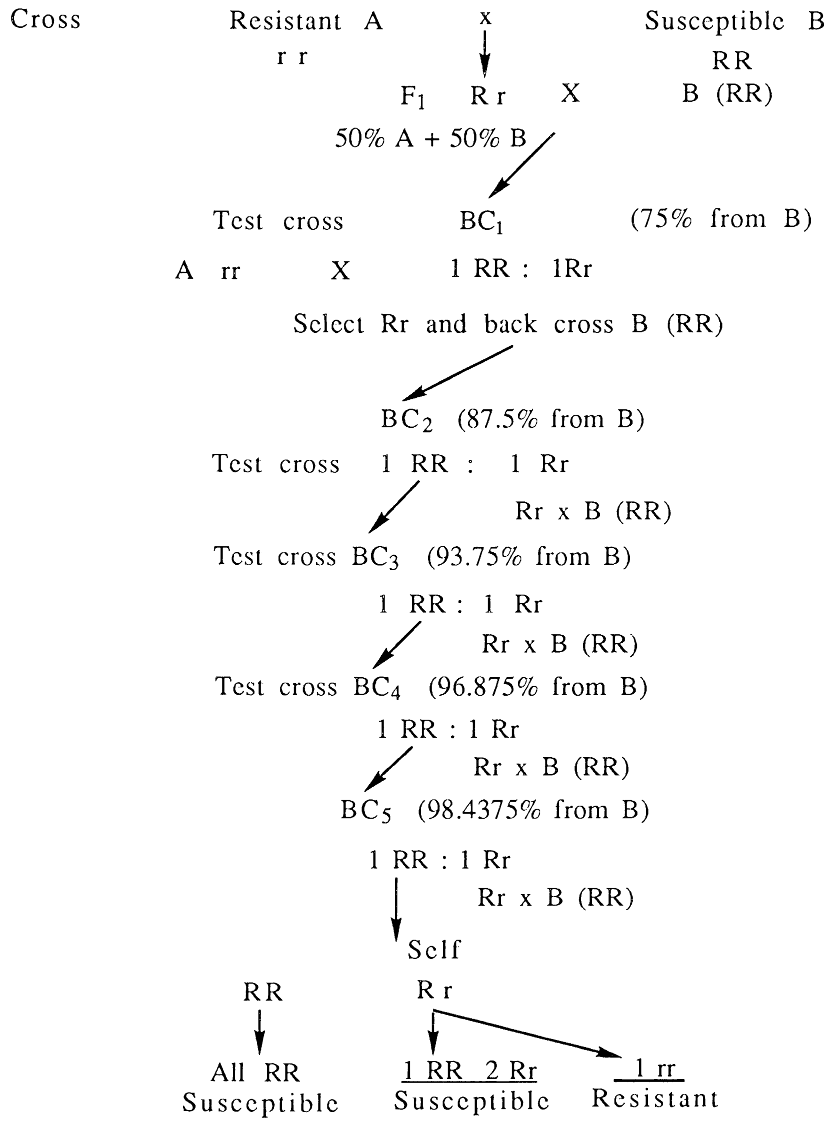

Fig. 14. Transfer of a recessive gene for disease resistance via simultaneous backcrossing and test crossing.

Mungbeans are selected on the basis of productivity, evenness in maturity, total growth, adaptability to seasons and resistance to diseases. A gene for yellow seed coat was identified and included in the selection program.

At AVRDC, powdery mildew is common in spring and autumn season crops when the weather is cool and dry. During summer, when the weather is hot and humid, *Cercospora*, leaf spot is widely prevalent. The segregating generations are subjected alternatively to these diseases in order to select for combined resistance. Photoperiod and temperature variations during these seasons permit selection for these environmental stresses.

The AVRDC ideotype for mungbean is a monocrop with yield of 3 t/ha at maturity of 70 days (57.1 kg/ha/day) under optimum environmental and cultural conditions. This assumes having 20 pods/plant, 10 seeds per pod, 6 gm per 100 seed, and a plant population density of

250,000 to 400,000 plants/ha. To have sufficient "source", a rapid and vigorous vegetative growth is needed. The characters visualized to attain this goal are rapid seedling growth, dark green lanceolate leaflets, no branching, a strong erect stem, vigorous root system, abundant nodulation, extended photosynthesis, a vegetative/reproductive ratio of 4 : 3, high and efficient photosynthesis, and efficient translocation of the photosynthates. To obtain better distribution of the "sink" would require a high harvest-index with a large number of nodes and short internodes, multiple peduncles at each node with abundant pods per cluster, synchronized flowering and ripening, nonshattering, pods above the seed canopy, large number of seeds per pod, and large seeds. For yield stability, resistance to diseases and insects, tolerance to temperature and moisture stresses, and resistance to seed weathering are needed.

Mungbean yield potential has been more than doubled in breeding lines at AVRDC employing a multidisciplinary breeding approach. Plant architecture is being altered to provide for more pods exposed above the canopy and more synchronous maturity. There is also progress in obtaining less sensitivity to photoperiod and temperature and resistance to multiple diseases.

4. Vegetable Soybean

Introduction, and selection of purelines were major breeding methods used in the development and release of vegetable soybeans. For example, in Taiwan, Tzuzunoko and Ryokkoh were two varieties introduced from Japan. The pod and seed quality, flavor and seed size were primary selection criteria. For Japanese market the characteristics described earlier are the most important characteristics the breeders look for. Selection for 'holding ability', i.e. how long the line can remain in harvestable condition is quite important for the processors.

In Vegetable soybeans the terminal node or the penultimate node or both appear to be without pods. However, the trait is quite variable within the population and it varies with season. Therefore, as a selection criteria it is not a dependable trait.

Pod length and pod width are significantly positively associated with seed size. Therefore, one can select at R_5 stage for the seed size.

If crosses are made between large seeded vegetable types and small or medium seeded grain type in order to derive a vegetable type with large seed through straight inbreeding, it is essential to have very large population size. Even then it is likely that all the desirable characteristics of the vegetable types could not be combined in the selections. Results of such straight cross suggest that at least two to three back crosses to vegetable types following the initial cross is desirable to quickly recover vegetable types with all desirable traits.

Narrow leaflet gene appears to be either tightly linked or it has a pleiotropic effect to produce higher percentage of two and more seeded pods. Therefore, at present attempts are being made to incorporate the narrow leaflet gene (lnln) into the vegetable soybean types since the Japanese market prefers two and three seeded pods. However, when the leaves are narrow, especially with small leaf size, foliage do not fully protect the developing pods. As a result the pods which are exposed to sun develop anthocyanin pigments on the green pod wall which is undesirable for the market. Therefore, large size narrow leaflet type with large leaf area are being selected. Genetic variation is also observed for anthocyanin pigment formation on the pod wall.

Vegetable soybeans are also used like shelled peas; the beans are shelled and marketed either fresh or frozen. The number of seeds per pod is not very critical for such soybeans.

But easy to shell and clean for marketing combined with high yield potential are some important selection criteria. From quality point of view large seed size, bright green color with good appearance, flavor and taste are used for selection. A sample data collection sheet is give in Table 7.

Average graded pod yield, in farmer's field, varies from 3 to 5 t/ha in Taiwan depending upon the season and genotype. The newly improved variety, KS # 1 has an average yield of 3 to 7.5 t/ha in different seasons. In experimental conditions new breeding lines exhibit a potential to produce upto 12 t/ha graded pod yield.

BREEDING ACHIEVEMENTS—SELECTED IMPROVED VARIETIES

1.Snap Bean

For frozen bean, variety Tendercrop released in 1955 in the USA is still used today. In 1970, 46% of the bush type green-podded beans had Tendercrop in their ancestry. The pods of Tendercrop are large, fleshy, bright green, smooth, straight, round and has a slow rate of seed and fiber development (good 'holding ability'). It has concentrated pod maturity.

White seeded Early Gallatin is an excellent canning variety. For fresh market OSU-1640 is an excellent variety. It gives a yield of 20-25 t/ha. Earligreen, Earliwax, Slendergreen, Slimgreen, Improved Tendergreen have been developed by a private company and are quite popular.

Some of the germplasm carrying special traits are listed in Table 8.

Table 8. Germplasm with special characteristics.

Name or No.	Character (s) or (Resistant to)
Tendercrop	Known for its plant type
Blue Lake	known for pod quality
PI 165426	Small leaf size, resistant to rhizoctonia root rot, root-knot nematode
Apollo	Resistant to curly top virus
Blue Mountain	Resistant to curly top virus
Gold Crop	Resistant to curly top virus
Wonder green	Resistant to curly top virus
PR-190	Rust
BARC-1	Rust
8 BP-3	Rust, anthracnose
Resisto	Rust
BBSR-13	Rust, haloblight
BRR-46	Pythium and *Aphanomyces* rot
RRR-36	Pythium and *Aphanomyces* rot
Noorinbee	Haloblight
RH-13	Haloblight
HB-76-1	Haloblight
Epoch	Brown spot
Viva Pink	Highest rate of N_2 fixation
5BP-7	Heat tolerant

Table 7. Vegetable soybean data sheet.

Experiment : Vegetable Soybean Location :

Note : Data Collection Sheet Date Sown

F. #	Cross	Pedigree	No. Har.	FPL	Flower		Maturity		Br.	Node	Pod No./5 P			Pod Wt./5P		
					C	Day	Ht.	Day			1S	2S	3S	1S	2S	3S

Lp		WP		Pod No./500g			Yield			SW/500 g	100 wt.	Damage Pod		W/Pod or W/o Pod		Lod	Color	Remarks
2S	3S	2S	3S	2S	3S	Total	PW	SPW	TW			Pod No.	Pod Wt.	Top Node	Two Node			

Remarks: 1. FPL=Length from bottom to first pod; 2. C=Color; 3. LP=Length of pod; 4. WP=Pod width ; 5. PW=Pod weight; 6. SPW=Standard pod weight;
7. TW=Total weight (leaf, pod and stem); 8. SW=Seed weight; 9. W/Pod=With pod; 10. W/o pod=without pod.

2. Peas

Round or wrinkled seed coats; yellow and green cotyledon are the key characters distinguishing the varieties. Varieties are also grouped according to plant height (bush or dwarf, medium tall, and tall); according to maturity (early, medium and late), to use of pods (fresh market, freezing, canning and dehydration).

Some of the major cultivars and their characters are given in Table 9.

Table 9. Major pea cultivars and their traits.

Cultivar	Shelling percentage	Use	Others
Alaska	42	Canning	
Early Superb	40	Canning	Dwarf
Meteor	45		
Badger	40	Fresh market, Dehydration	Dwarf
Little Marvel	40	Sweet, fresh market	Dwarf
Bonneville	45		Medium tall
Lincoln	45	Canning	Dwarf to medium tall
Delwiche Commando	45		Medium tall
Thomas Laxton		General purpose freezing	
Sylvia		Edible podded	Tall
Heymuu		For Tender leaves	Branching type
Sugar Snap		For Tender leaves	Branching type

Early Sweet or Alsweet is replacing Alaska. Alsweet has higher yields due to more double pods. Seeds are wrinkled.

In Taiwan recently the edible podded pea is becoming popular.

For tender green leaves, quick growing and easily branching types with crisp tender tips and first leaves are preferred. Heymuu and Sugar Snap varieties meet these qualifications.

3. Mungbean

India has done considerable research on mungbean through their "Pulse Scheme" since 1943. In 1967 an All-India coordinated Pulse Improvement Program commenced. Yield and disease resistance were the primary concerns. A number of varieties have been released (Table 10).

In the Philippines synchronized maturity, seasonal adaptation and high yield along with disease resistance was emphasized. BPI at the Economic Gardens and the University of the Philippines at Los Banos conduct research and release new varieties.

Indonesia, Thailand, U.S.A. , Sri Lanka and Australia have mungbean breeding program and they have released new improved varieties that are high yielding, carrying resistance to powdery mildew, cercospora leaf spot, synchronized maturity and large seed size. A list of varieties released in different countries from AVRDC materials are given in Table 11.

Table 10. Mungbean cultivars released in India.

Cultivar name	Source/ parents	Year	Location	Maturity (days)	Improved characters[1]	References[2]
I. Developed as selections						
Type 1	Muzaffarpur	1948	U.P.	60	G, GM	1
Shining Mung No. 1	Kulu Mung Type 1		Punjab	65	LG, S	2
CO1	Local	1952	Tamilnadu	135	SG, DL	3
CO2	PLS 365/3	1975	Tamilnadu	65	DG	4
CO3	PLS 367	1976	Tamilnadu	70	SG, IRC	4
BR-2	Bhagalpur Local		Bihar	110-115	MG	5
Amrit	Bihar Local		Bihar	90	MY,YMV	5
Khargone-1	K 119-56		M.P.	65	LG, GM	5
R-288-8	Local		Rajasthan	70-75	SG	5
Krishna-11	Gwalior Local		M.P.	65	LG, GM	5
D66-26	Local	1968	Rajasthan	60-65	SG	5
Pusa-Baisakhi	Type 44		New Delhi	60-65	DG, spring and summer	5
Kopergaon	Local	1975	Maharashtra	60	SG	6
II. Developed by hybridization and selection						
Type 44	Type 1 x Type 49	1948	U.P.	60-65	DG, summer, spring	7
Type 51	4465-4 x Type 49	1962	U.P.	75-80	SG, mixed crop	8
Jawahar-45	Madira x UP local	1972	M.P.	75-80	SG,Kharif	9
S-8 (Mohini)	BR 2 x T 2	1972	New Delhi	60-65	SG	10
Kanke Multi-purpose	T1 x China Moong 781	1973		-	SG	11
ML1	Hyb. 45 x p 23-67	1973	Punjab	90	G, tolerant to disease	12
KM 1	S 8 x PS 16	1978	Tamilnadu	65	YMV, pod borer	5
ML5	No. 54 x Hyb. 45		Punjab	80-85	G, Kharif	5
PS 7	-	1981	New Delhi	60-65	DG, summer	5
PS 10	-	1981	New Delhi	60-65	DG, summer	5

[1] G: Green seed; GM: For green manure; LG: Light green seed; SG: Shining green seed; S: Shining seed; DG: Dull seed; DL; Dry land; IRC: Irrigated conditions; MG: Mottled green seed; MY: Mottled yellow; YMV: Yellow mosaic virus tolerant.

[2] 1. S.P. Singh, 1955; 2. S.G. Singh, 1965; 3. Premsekar and Srinivasan, 1961; 4. Rathnaswamy et al., 1977; 5. D.P. Singh, 1982; 6. Mandoli and Nigam, 1966; 7. Pathak and Singh, 1961; 8. Pathak et al., 1962; 9. L. Singh et al., 1972; 10. S.P. Singh, 1972; 11. Bhargava, 1973; 12. S. Singh et al., 1973.

Table 11. AVRDC mungbean selections released as cultivars in different countries.

Cultivar	AVRDC no.	Year of release	Country	Improved characters[1]
ASVEG 78	VC 1089-A	1978	Costa Rica	HY
Bangasa	V 3476	1980	Korea	HY, UM, LR
Tainan Sel. #3	VC 1628A	1981	Taiwan	HY, UM, LR
M 986		1981	India	
	VC 1560D[2]	1982	Australia	
King	V 1388[2]	1982	Australia	HY, EM, PW. LR
Station 46	VC 1000-45-B	1982	Fiji	HY
Seonhwa Nogdu	VC 1973-A	1982	Korea	HY, MMV, RPM, (CLS), UM
Type 77	VC 1131-B-12-2B	1982	Sri Lanka	HY, MYMV, CR
Manyar	VC 1089-A	1983	Indonesia	HY, CLS, R
Nuri	V 2773	1983	Indonesia	HY, (CLS), R
		1983	Malaysia[3]	
Imara	V 1380	1983	Tanzania	
Station 25	VC 1007-14-1-5B[3]	1984	Fiji	
Station 27	VC 1160-1-1-2B[3]	1984	Fiji	
BPI Mg2	VC 1163	1984	Philippines	HY, CLS, RPM, R
Xu Yin No. 1	VC 1973-A	1985	China	HY, WA
Boliche 451	VC 1163[3]	1985	Ecuador	
KPS No. 1	VC 1973-A	1985	Thailand	
KPS No. 2	VC 2778-A	1986	Thailand	
Walet	VC 1163-A	1986	Indonesia	HY, NS, CLS, RPM, TDO, UM
Gelatik	VC 1160-22-2B-1-B	1986	Indonesia	HY, NS, CLS, RPM,UM
BPI Mg4	VC 2764-B	1986	Philippines	HY, UM, LR, EM, (CLS), RPM
DX 102a	VC 2768-A	1986	Vietnam	HY, SLS- R, RLD
DX 113	VC 2763-A	1986	Vietnam	HY, TASS, RLD

[1] HY: High yield; UM: Uniform maturity; LR: Lodging resistant; EM: Early maturing; PW: Resistant to pod weathering; CLS/ (CLS) : Resistant/moderate resistant to *Cercospora* leaf spot; RLD: Resistant to local diseases; SLS-R: Sandy loam soil after rice; TDO: Tolerance to damping off; R: Rust resistant; MMV: Resistant to mungbean mottle virus; RPM: Resistant to powdery mildew; MYMV: Resistant to mungbean yellow mosaic virus; CR: Resistant to charcoal rot; WA: Wide adaptability; TASS: Tolerant to acidic and saline soils; NS: Non-shattering.

[2] Adapted selection developed from AVRDC parental stocks.

[3] Reported release but no further information.

Through intensive research efforts at AVRDC in collaboration with the national program scientists the yield potential of mungbean has been improved from 0.5 t/ha to more than 2 t/ha. Photoperiod insensitivity, multiple disease resistance, large seed size and synchronized maturity have been incorporated in improved lines.

4. Vegetable Soybean

The most popular vegetable soybeans in Japan are predominantly developed by private seed companies. Among 50 new vegetable soybeans, the most popular ones are : Tzuzunoko, Ryokkoh, Kegon, Hatsutaka, Taisho Shiroge, Nakate Kaori, Suzumo, Enrei, Fukuda, Raityo, Shirobato, Tamasudare, Hakutyo, Shiratsuyu, and Blue Side.

In Taiwan at present the leading varieties are Kaohsiung No. 1, Tzuzunoko and Ryokkoh. Kaohsiung No. 1 (KS # 1) is a pure line selection from Taisho Shiroge from Japan done at AVRDC. Detailed trials and final assessment for release was done by Kaohsiung DAIS. KS # 1 was released in 1987. In 1988 it occupied 51% of the total vegetable soybean area in Taiwan. In 1989, it is expected to occupy more than 80% of the area.

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果 樹 育 種 概 論

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前 言

果樹為一種世代長、樹體較大，佔地面積大之作物。一般而言具有高度異質結合之遺傳特性。生長發育上，木本果樹，除植株高大外，尚有幼年期較長不利育種之因素，因此，從開始選育到新品種命名推廣栽植，至少需要十年以上，倘能研究改進果樹之技術層面著手，建立科學化之育種程序和相應之育種制度，以提高育種效率，自然可加速育種過程。

數十年來，台灣地區之果樹品種改良顯有卓著之成就，才能建立目前之水果產業，然而過去之成就大都建立在引種馴化而達到利用的基礎上，幾乎未曾從此基礎上繼續運用其他之品種改良策略，將此既有之材料發揮光大，開發本地之品種，從此觀點而言，本省果樹產業實際上是處在開發中之階段，實在有必要加以檢討，突破現狀以建立先進果樹產業國家之基礎。

果樹育種之程序

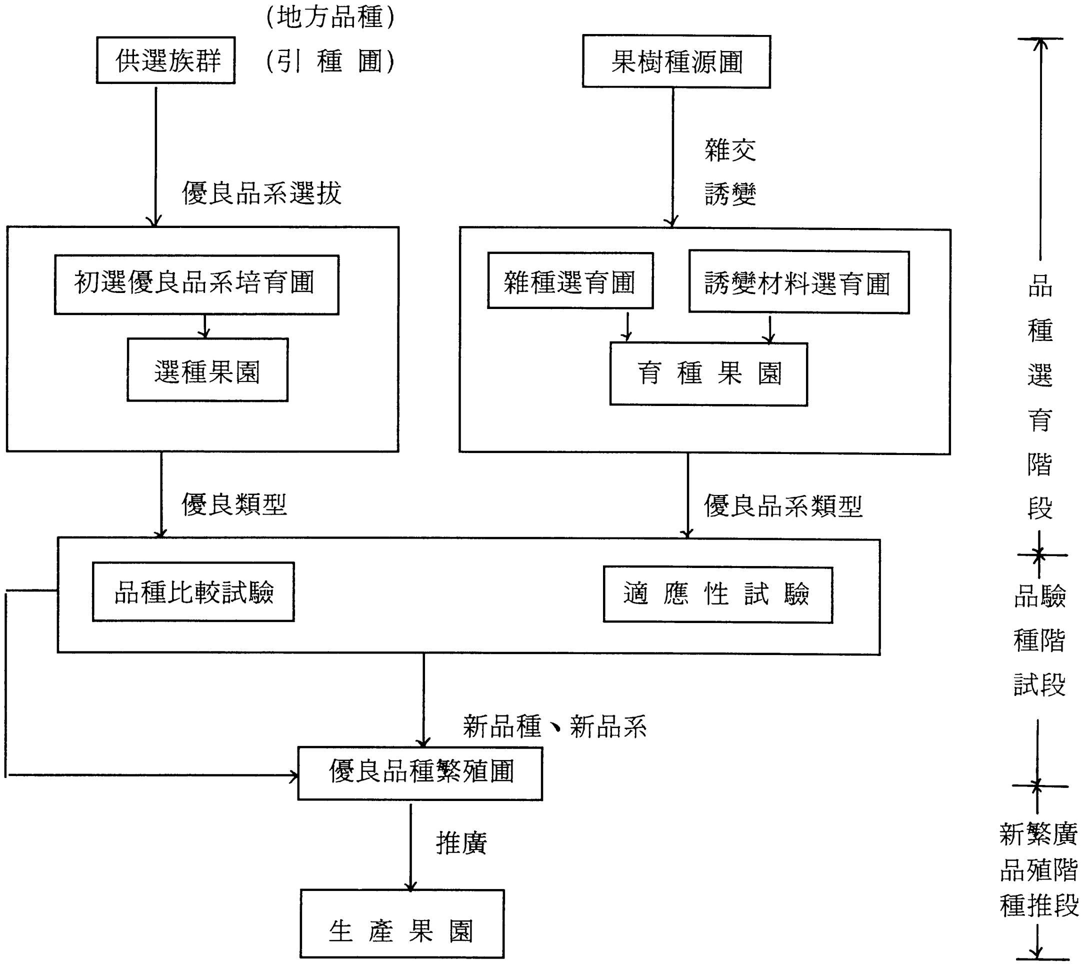
一、育種之程序

通常從選育到新品種應用於果樹產業要經過選育、試驗及繁殖推廣三個階段，其程序大致可用圖一表示。

二、加速育種過程之途徑

將育種程序作為一種制度，以保證多、快、好、省地育出新品種，並使其在生產中發揮作用。在育種過程中曾經出現過太慎重，使得新品種的命名推廣延遲。相反地也發生比較粗糙，以致命名的新品種對果樹產業毫無助益而被淘汰。因此對育種程序應本著慎重的能度，採取科學化的原則，重視質量的前提下，儘可能設法縮短育種的期間，加速育種的過程與效率。主要的途徑可歸納於下:

1.明確育種目標和充分利用果樹種源。
2.儘可能瞭解與掌握育種性狀的遺傳規律。
3.提高早期性狀鑑定的效果。
4.加速雜交後代或選獲優良品系嫁接苗進入結果期。
5.提早加速繁殖。
6.靈活運用育種程序。
7.提高育種程序中各階段的工作效率。



圖一 果樹育種程序

無性繁殖果樹種類之育種方法

一般而言，無性繁殖之果樹其育種方法可採取，引種、營養系選種、實生選種、雜交育種、誘變育種及多倍體育種等。本文僅就引種、選種及雜交育種等之育種程序中之選育階段的技術及原則作一概略之介紹。

一、引 種

1.引種的概念

果樹樹種(species)和品種(variety)在自然界都有它一定的分佈範圍。把果樹品種從原有分佈範圍引入新的地區栽培稱之爲引種。

果樹引種可能發生兩種反應情況：一種是原分佈地區和引入地區自然差異較小，或由於引種植物之適應性强，以致不改變遺傳性也能適應新的環境條件，其中包括採取某些措施，使引入植物能正常地生長發育和開花結果，這叫做簡單引種。另一種是原分佈區和引入地區

的自然條件差異較大或由於引種植物的適應能力較弱，只有改變其遺傳性才能適應新的環境，這叫做馴化引種。

對無性繁殖的果樹而言，簡單引種和馴化引種兩者之間有著明確的界限。前者引入接穗或其他無性繁殖材料，而後者必須採用種子。

2.引種之生態因素

植物生態學是研究植物與自然環境、栽培條件相互關係的科學。從事引種時，可從兩方面考慮:

(1)綜合生態因子

據日本菊池秋雄(1953)等研究，世界果樹的主要產區可以根據綜合生態因子分爲夏乾帶，夏濕帶和介於兩者之間的中間帶(表1)。屬於同一生態地區的不同產地的品種在氣候適應性上具有較多的共通性，相互引種，比從不同生態型地區引種成功的可能性較大。

表1. 生態型劃分的果樹產區

(菊池秋雄. 1953)

生態型劃分	代表地區	氣候因子			果樹種類
		夏半期雨量(年雨量)mm	平均氣溫℃ 一月	平均氣溫℃ 七月	
夏乾帶	地中海沿岸地區西班牙南部、法國、意大利、巴爾幹半島、小亞細亞沿海地區、北非沿海地區	90-270 (400-830)	6-9	23-27	歐洲葡萄、西洋梨、歐洲李、甜櫻桃、酸櫻桃、南歐系桃、歐洲杏、巴旦杏、榲桲、歐洲栗、枸櫞、檸檬、甜橙、酸橙、無花果等。
夏乾帶	美國加州地區、美國加州及俄勒岡州南部	40- 80 (300-500)	9-13	22	歐洲葡萄、西洋梨、南歐系桃、歐洲杏、歐洲李、核桃、無花果、甜櫻桃、蘋果、檸檬、臍橙、葡萄柚等。
夏乾帶	伊朗、土耳其、阿富汗、蘇聯的中亞細亞各地、蒙古、中國新疆及內蒙古等地。	30- 66 (90-250)	0.8 | 1.1	26-29	核桃、石榴、蘋果、西洋梨、榲桲、無花果、桃、杏、李、歐洲李、歐洲葡萄、巴旦杏、阿月渾子等。
中間帶	中國東北南部、華北各省，陝西甘肅、寧夏及江蘇、河南、安徽的北部、內蒙古、新疆的南部	400-500 (450-600)	- 5 | 1	24-27	蘋果、秋子梨、白梨、桃、杏、中國櫻桃、山楂、板栗、棗、柿、海棠等。

生態型劃分	代表地區	氣候因子			果樹種類
		夏半期雨量 (年雨量)mm	平均氣溫℃		
			一月	七月	
中間帶	韓國北部	800-1000 (900-1300)	-4 | 2	23-26	蘋果、秋子梨、白梨、桃、杏、柿、歐洲葡萄、中國栗、日本梨、核桃等。
	日本本洲北部各縣及北海道	500-800 (1000-1200)	-6 | 1.2	21-25	蘋果、歐洲櫻桃、西洋梨、沙梨、李、杏、美洲葡萄、歐洲葡萄、柿、日本栗、核桃等。
	歐洲大陸東南部、英國、瑞士、德國、法國、波蘭、奧地利	300-500 (600-900)	0-4	17-19	蘋果、歐洲葡萄、西洋梨、歐洲櫻桃、桃、油桃等。
	美洲東部、大西洋沿岸、華盛頓、紐約、波士頓往北到加拿大、西部的華盛頓州、俄勒岡州等各地	東部 500 (1000) 西部 200-220 (800-1000)	-1.4 | 1.4 4	22-24 17-19	蘋果、西洋梨、美洲葡萄、長山核桃、桃、李、杏等。
夏濕帶	亞洲大陸東南部、中國長江流域一帶、朝鮮半島南端	800-900 (1000-1200)	4-6	27-29	梅、楊梅、枇杷、柑桔類、中國櫻桃、石榴、銀杏、板栗、沙梨、李、棗、蘋果、沙果、葡萄等。
	日本南部沿海地區、四國、九州及本州南半部	800-1800 (1000-2400)	3 | 5.5	26-27	沙梨、桃、李、梅、柿、枇杷、柑桔類、日本栗、美洲葡萄等。
	美國東南部包括佛羅里達、喬治亞、阿拉巴馬、密西西比、路易斯安那、得克薩斯等州	600-1000 (1000-1600)	10 | 18	27-28	甜橙、葡萄柚、美洲葡萄、西洋梨、雜種梨、桃等。

(2)個別生態因子

a.溫度：通常冬季氣溫過低或夏季氣溫不足限制果樹北引，而冬季或夏季氣溫過高則限制

果樹的南移，溫度條件不適合對引種植物的不良影響可歸納爲兩方面：(a).溫度條件不符合生長發育的基本要求而致使引種植物不能正常生存，或高溫低溫對樹體及其不同部位器官造成致命傷害；(b).引種植物雖能正常生存，但由於溫度條件不適影響果實的產量與品質，使引種植物不具經濟栽培價值。

b.光照：對果樹引種的影響包括日照强度、時間、和光週期。

c.降水和濕度：果樹引種時應考慮樹種的需水量、抗旱能力及引種地區的降水量分佈。

d.土壤：土壤的持水力、透氣性、含鹽量、PH值、及地下水位的高低都能影響果樹種類和品種的分佈，引種時必須因地制宜，充分注意品種類型間的抗耐性差異。

e.其他生態因子：包括目前難以控制的病蟲害，品種間抗風力的差異。

上述個別生態因子在引種時既要別分析，也要綜合地去研究和引種適應性的關係。

3.引種的原則

選擇引種材料的原則有二：一爲對引種材料經濟性狀的要求，二爲引種材料對當地風土條件適應的可能性。

4.引種的方法

(1).簡單引種

其方法可概括爲：少量引種、多點試驗、全面鑑定、摸索規律、加速繁殖、逐 步推廣。

引種試驗時應注意的幾個環節:

a.嚴格檢疫和編號登記制度。

b.引種材料可透過調查、收集、通信郵寄、購買與相互交換等方式引入。

c.可以高接法與對比法加速引種鑑定的過程。

(2).馴化引種

馴化引種和簡單引種在方法上最大的區別在於，馴化引種必須從實生苗開始，以較大的個體數量，透過有性繁殖過程，發生基因的分離重組，給選擇適應性更强的類型提供了可能性。

在選擇引種地區和引入類型時，基本上可參考簡單引種。

在種源選擇上，應不少於五個。都應處于或接近樹種分佈極限的邊緣地帶。提供選拔的實生族群宜大。

當引種之品種類型的適應能力和當地環境條件差距較大，一個世代無法馴化，就需要採取多代連續馴化法和逐代遷移馴化法。

5.結　論

引種工作的成敗包括兩項因素:

(1).內在因素：選擇適當的基因型使能滿足引種地區生態環境的要求。

(2).外在因素：採取適當的農業技術措施使引入類型能夠正常地生長結果提供符合要求的產品。

兩者相輔相成，不能偏廢。

二、選　種

1.實生選種

(1).實生選種的概念

對實生繁殖產生的自然變異進行選拔，以改進果樹族群的遺傳組成，或從中選出營養系品種稱爲果樹實生選種。

(2).實生繁殖的變異

果樹是高度異質結合且多屬異花授粉的植物，因此在實生繁殖的情況下常產生複雜多樣的變異。

果樹實生族群內個體的變異主要由基因重組、突變和環境變異(modification)所引起：

a.基因重組：實生選種中選拔的表現優異的基因型可能包括基因重組產生的兩類不同效應。

(a).基因的加性效應：由來自不同親本控制同一經濟性狀的有利基因的累加，從而產生加性效應優於親本的遺傳型。

(b).基因的互作效應：由基因間顯性，上位性等互作效應而產生的超親的新特性。也就是由新的有利的非加性效應所引起。

b.突變：廣義的突變包括染色體的數量和結構的變異。

c.環境變異：由環境條件改變所引起的表現型變異屬於非遺傳的變異。

(3).選拔的作用

選拔就是選優去劣，是各種育種途徑中不可缺少的環節。

自然選拔的作用在於定向地改變族群的基因頻率，促進生物不斷地進化，產生對自然環境高度適應的新類型；變種乃至新的物種(species)。

人工選拔的作用則是選擇合乎人類需要的經濟性狀的變異，促進繼續發展爲更符合現代農業生產要求的新品種。

(4).選拔的種類

a.一次選拔和多次選拔

b.直接選拔和間接選拔

c.混合選拔、集團選拔和單株選拔

d.獨立淘汰選拔和性狀加權選拔

(5).營養系果樹實生選種程序

a.報種和預選：採取鼓勵各地果農選報優良品系，配合農試研究機構評選的辦法，預列初選的侯選樹。

b.初選：研究人員對預選樹在現場調查記載後，採集果實樣品進行調查記載，並對所記載資料進行整理和分析比較，經連續2～3年預選樹進行產量、品質、抗逆性等的複核鑑定。根據選種標準，將表現優異的預選樹，確定爲初選優良母樹對初選優良母樹要及時嫁接繁殖30～50株以上，作爲選種圃和多點生產鑑定的實驗樹。在觀察母株的同時，調查營養系後代的表現。在不影響母株生長結果的前提下，亦可對附近的低劣樹進行高接更新，如此可提早結果，並達到高接鑑定的作用。

c.複選：選種圃裡的嫁接樹，結實後經三年的後代比較鑑定，連同對母樹，高接樹和多點

生產鑑定樹的系統調查材料，經過果農和農試研究人員的評鑑，即可進一步評價初選的優良母樹複選更優良的母樹，提供建立推廣用之接穗母樹園。

(6).結　論

實生選種的原則，簡單地說即優良品系就地利用和邊利用，邊鑑定，在利用中求提高選種的效率。

2.芽變選種

(1).芽變選種的意義

芽變是體細胞突變的一種。突變發生在芽的分生組織細胞中，當芽萌發長成枝條，並在性狀上表現出與原類型不同，即爲芽變。芽變包括由突變的芽發育成的枝條和繁殖而成的單株變異。

芽變是植物產生新變異的無限豐富資源，它既可爲雜交育種提供新的種質資源，又可直接從中選出優良的新品種，是選育新品種的一種簡易而有效的方法。

果樹芽變選種中有名的例子，如元帥係蘋果的芽變選種，溫州蜜柑的芽變選種，育出早熟型和適宜加工製罐的變異等。

(2).芽變的特點

芽變是遺傳物質的突變，表現出多種多樣，極其複雜。

主要特點如下:

A.芽變表現的多樣性

有形態特徵的變異，也有生物學特性的變異。

(A).形態特性

a.葉的形態變異：柑桔中有大葉與小葉，寬葉與窄葉的變異，鳳梨中有葉片無刺的變異。

b.果實的形態變異：變異包括果實大小、形狀、果皮厚薄、光滑程度、色相與色調等。

c.枝條的形態變異：無刺的溫州蜜柑上出現有刺的枝條，黑莓有無刺的變異。

d.植株的形態變異：短枝型芽變。

(B).生物學特性

包括生長與結果習性、物候期、果實品質、抗性和育性。

a.生長與結果習性的變異

包括枝條的橫生長與縱生長，短枝所佔比率，分枝角度，果枝形成的習性及連續結果的能力等。

b.物候期的變異

包括萌芽期，開花期及果實成熟期。

c.果實品質的變異

例如甜紅玉蘋果是紅玉的芽變：蘋果緊湊型芽變，除株型發生變異外，果實的風味也往往發生變異，多數變淡。

d.抗性的變異

柑桔中經常發現有不同程度抗寒的變異類型。

e.育性的變異

包括無籽、雄性不育、和單性結實的變異。如蘋果和葡萄的無籽變異；甜橙、桔子中雄性不育的變異。

B.芽變的穩定性

可概括地分成三點說明：

(A).穩定的芽變：性狀一經發生改變，在其生命周期中可長期保存，並且無論採用何種繁殖方法都能把變異的性狀遺傳下去。

(B).無性繁殖下保持穩定的芽變：當採用有性繁殖時或發生性狀分離，或全部後代又恢復成原有的類型。

(C).回歸突變：雖不經繁殖，但在其繼續生長發育過程中，失去已變異的性狀，恢復成原有的類型。

芽變的穩定性和不穩定性的實質，或與基因突變的可塑性，或與突變的嵌合結構有關。

C.芽變性狀的局限性和多效性

(A).芽變性狀的局限性

芽變一般是少數性狀發生變異，是因爲沒有發生遺傳物質的重組，僅僅是原類型遺傳物質的突變，包括基因突變與染色體變異，這些突變所能引起的變異性狀當然是有局限性的。

(B).芽變性狀的多效性

少數芽變發生變異的性狀有幾十個。例如蘋果的短枝型芽變，由于枝條節間短，所以枝條變短粗樹冠也表現矮化，並且比較早結果且豐產，另外伴隨枝條角度變小，樹冠直立，或是夾角變大樹冠開張。

這一現象的解釋有兩種:

a.芽變是由于染色體的缺失所造成。

b.可能是幾個鄰近基因同時發生了突變。

(3).芽變的細胞學和遺傳學基礎

A.嵌合體(chimera)與芽變的發生

(A).嵌合體(chimera)

被子植物枝梢頂端分生組織都有相互區分的組織發生層，用LⅠ、LⅡ、LⅢ 表示。植物的組織即由這三層細胞分化形成。在正常的情況下，這三層細胞具有相同的遺傳組成。如果層間與層內不同部分之間發生體細胞變異，致含有不同的遺傳物質，這種情況就叫做嵌合體。層間不同的叫做周緣嵌合體。層內不同的叫做扇形嵌合體。

(B).枝梢頂端分生組織的分裂與分化

a.LⅠ細胞行垂周分裂，形成一層細胞分化爲表皮。

b.LⅡ細胞行垂周和平周分裂，形成多層細胞，分化爲皮層的外層及包原組織。

c.LⅢ的細胞分裂與LⅡ相似，也形成多層細胞分化為皮層的內層及中柱。

(C).芽變的發生

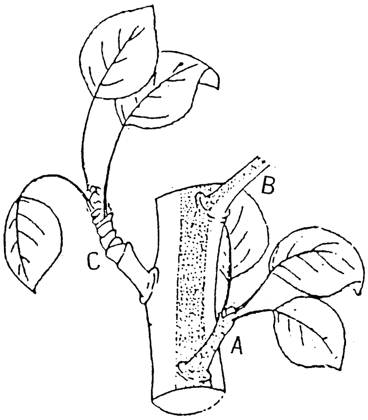
芽變是細胞中遺傳物質的突變，但是只有枝梢頂端組織發生層的細胞發生突變時，將來才有可能成為一個芽變。

突變發生在LⅠ，則表皮就會出現變異；發生在LⅡ，皮層的外層及包原組織就會出現變異；發生在LⅢ，皮層的內層和中柱就會出現變異。

一般情況下，只有個別層中的幾個細胞發生突變，三層同時發生同一突變的情況幾乎是不可能的。因此芽變開始發生時總是以嵌合體的形式出現。

(D).芽變的轉化

a.嵌合體的自然轉化，如圖二所示



圖二、嵌合體的自然轉化
(a).由扇形嵌合體長出的周緣嵌合體枝。
(b).由扇形嵌合體長出的扇形嵌合體枝。
(c).由扇形嵌合體長出的非嵌合體枝。

b.層間取代

芽變嵌合體常常由於突變部分與未變部分的競爭，一方排擠另一方，最後取而代之。有時外部的原因也會造成這種改變。這種轉化現象稱之為層間取代。如2-2-4回復2-2-2，4-4-2變成4-4-4的同質突變體。

c.芽變在無性世代中所以表現不穩定，其主要原因之一就是層間取代造成的。

(a).改變遺傳物質的突變：如進行輻射育種時，輻射的作用之一，是使染色體發生結構重排，或是使基因發生突變。

(b).未改變遺傳物質的突變：通過輻射，殺死外層細胞，由深層取代外層，如果深層原來就與外層不同當然就會出現新的變異類型。當果樹遭受凍害或其他傷害之後，由于正常枝條受到凍害或其他傷害而死亡，不定芽由深層萌發出來，就與外層不同，如果該樹種原來是中周或內周嵌合體，就可能表現為同質變體。

(E).芽變的遺傳

a.芽變的遺傳類別

(a).染色體數目變異：包括多倍性，單倍性及非整倍性。

(b).染色體結構重排：包括易位、倒位、重複及缺失。

(b).基因突變：包括眞正的點突變及組碼移動突變。

b.芽變系間交配的親和性

同一個來源營養系的不同芽變品種，相互交配以後其著果率和種子數都顯著低於不同營養系的品種間雜交，而與自花授粉極爲相似。

同源四倍體之芽變品種常常表現較高的自交結實率。

c.正突變與逆突變

(a).正突變：由顯性變成隱性(A → a)

以一對基因爲例，異花授粉的果樹，正突變的形式包括 AA → Aa和Aa → aa。前者的性狀在當代不能表現，後者卻可以表現。在不完全顯性的情況下，或是在基因產生加性效應的情況下，AA → Aa或Aa → AA(逆突變)的突變都能在當代表現而且可以用無性繁殖，固定此突變性狀。

(b).逆突變：由隱性突變成顯性(a → A)

此種突變無論何種作物都能在當代表現出來。而果樹採用無性繁殖，一旦突變發生，性狀即可獲得穩定。例如桃果實的無毛變有毛，黃肉變白肉。

d.各組織發生層的遺傳效應

(a).LⅠ：比較單純，主要與表皮的性狀有關。如茸毛和針刺的有無。如黑莓無刺枝條之突變。

(b).LⅡ：果實與葉片色彩的突變。LⅡ層是包原組織的發生層，只有當一個突變包含LⅡ 時，它在有性繁殖的後代表現，在育種上才能發生效果。

(c).LⅢ：它是中柱組織發生層，從中柱可以長出不定芽的果樹。如果發生2-2-4或2-4-4的嵌合突變，由此中柱產生的不定芽即可得到 4-4-4 的同質突變體。根常常是從LⅢ深層組織長出的，經由根插也能得到同質突變類型。

(F).芽變選種的時期

芽變的選種，原則上應在整個生長發育過程的各個時期進行詳細的觀察和選拔。爲提高芽變選種的效率，還必須根據選種目標利用最容易發現芽變的有利時機，集中進行選拔。例如：

a.果實採收期：此時最容易發現果實經濟性狀的變異。如果實的著色時期、著色狀況、成熟期、果形、品質以及結果習性，豐產性等。

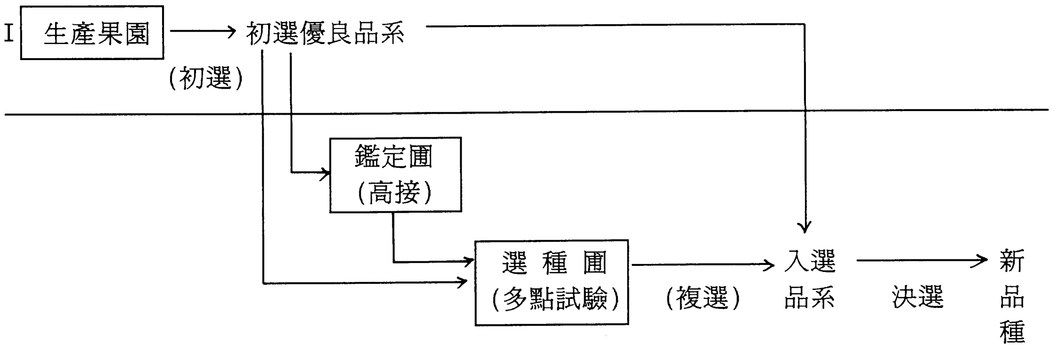
b.災害期：可由兩方面加以考慮

(a).在嚴重的自然災害之後，如霜害、風災、水災、乾旱和病蟲害，選拔抗性等特別强的變異。

(b).災害發生後，原有正常枝條受到損害，而使組織深層的潛伏變異表現出來。所以要注意從不定芽和萌蘖長成的枝條，選拔抗性的芽變 。

(G).芽變選種的程序和步驟

芽變選種分兩級進行。第一級是從生產果園初選優良品系，包括枝變，單株變異。第二級是對初選優良品系的無性繁殖後代比較篩選包括複選和決選兩個階段。選種程序如圖三



圖三、芽變選種程序

三、雜交育種

1.雜交育種的意義和特點

(1).雜交育種的意義

經由基因型不同的類型間配子的結合獲得雜種，對雜種進行培 育選拔以獲得新 的品種，稱之為雜交育種。它除了綜合雙親控制不同性狀的有利基因外，對同一性狀可發生兩種不同的效應：

A.加性效應：集中父母親本雙方有利的基因於雜種。

B.非加性效應：利用生態地理起源上距離較遠的品種類型間相互雜交，由於雜種雜交結合部位加多，產生雜種優勢，使其性狀超越雙親。

(2).果樹雜交育種的特點

任何一個果樹雜交育種既是組合育種，同時也是優勢育種。既綜合來自不同親本的優良基因，同時又利用了不同基因型配子間的良好配合力形成的雜種優勢。優良的基因組合無需經過分離純化，經由無性繁殖可以穩定地傳遞下去，不產生分離重組，而雜種優勢也可以穩定地保持下去，不發生解體而衰退。

2.雜交遺傳動態：

雜交育種成敗的關鍵在於根據性狀遺傳規律科學地選配親本。果樹育種最大的困難就在於對性狀的遺傳研究和瞭解太少。

(1).早熟性：品種從嫁接到開始結果經歷的時間稱為營養期 (vegetative period)。雜種從種子發芽到開始結果經歷的時間稱為幼年期 (juvenile period)。早熟性是指實生苗結實的特性。營養期短的親本，其雜種後代的幼年期也比較短。幼年期短的植株嫁接後營養期也比較短，早熟性通常多表現為多基因控制的數量性狀，雜種表現為連續變異。

(2).樹性：通常表現爲多基因控制的連續變異，樹性矮化程度有時還受到質量性狀單基因的影響，如桃、梅、櫻桃隱性垂枝性基因會使樹冠變小，桃的隱性矮化基因dw同質化後可使樹體極端矮化、節間大爲縮短。

(3).產量：是由若干個相對獨立遺傳的單位性狀構成的綜合性狀。在構成性狀中有許多基因控制的數量性狀，如花芽形成能力，果枝平均果實數，單果平均重等；也有由少數一、兩對基因控制的質量性狀，如單性花和完全花，雄性不孕性，自花結實性等。作爲綜合性狀的產量和構成性狀相比，遺傳力常顯著較低。育種中常比較重視對產量影響較大的構成性狀之遺傳力。如對桃產量影響較大的單果重遺傳力爲0.31，但產量遺傳力僅0.08。

(4).果實品質

是由若干個相對獨立遺傳的單位性狀，如糖、酸、芳香物質、果肉結構、果肉質地等構成的綜合性狀

A.含糖量：數量性狀，雜種常呈連續變異常態分佈。

B.含酸量：一般認爲屬于多基因控制的數量性狀。

C.芳香：某些酸類和醇類物質可使果肉帶有芳香。常由一對或少數幾對基因控制。香對無香爲不完全顯性，還常受到一些修飾基因的作用。

D.苦澀味物質如單寧、苦皮：可能由若干對基因抗制表現不完全顯性，也可能存在某種互作效應。

E.維他命C、脂肪、蛋白質、粗纖維含量等多屬數量性狀遺傳。

F.果肉質地：如桃的溶質對不溶質爲顯性，蘋果的綿質對脆質爲顯性。

(5).果實重量：典型的數量性狀。

(6).果實形狀：柑桔果形的變化較小，梨與蘋果則變化較大，A. G. Brown (1960)研究認爲蘋果果形爲數量性狀。野生類型的果形，在後代常有優勢的表現。桃的圓形桃對扁平形的蟠桃爲由一對基因控制的質量性狀。

(7).果實顏色：果實顏色主要由果皮、果肉、和果汁等花青素類的色素種類和數量的分布所決定，通常有色對無色、深色對淺色爲顯性或不完全顯性，由一對或少數幾對基因所控制。如蘋果果皮的紅色對綠色或黃色爲顯性。無彩色品質爲隱性同質結合。又如桃果肉白色對黃色爲顯性，由一對基因所控制。

(8).果實成熟期：多基因控制的數量性狀，雜種成熟期呈連續分佈。

3.果樹遺傳特點

(1).品種間雜種性狀的分離多樣複雜。

(2).雜種族群經濟性狀在有性後代中普遍退化。

(3).雜種族群若干性狀的趨中變異。如果實成熟期、果實形狀等性狀。

4.雜交親本的選擇和選配

正確地選擇和選配親本是育種工作成敗的關鍵。

(1).雜交親本的選擇

根據育種目標，從果樹種源或栽培品種中挑選最適合作爲親本的品種和類型。通常選擇親本時，總是針對育種目標選擇優良性狀多，不良性狀少的品種作爲親本。選擇時

應考慮下列幾點:

A.以重要性狀爲主

如罐桃育種中果肉的不溶質比果肉黃色更重要。豐產穩定生產比早熟性重要。因此權衡不溶質白肉比溶質黃肉類型作爲親本價值較大。

B.以多基因控制的綜合性狀爲主

選擇親本時，必須優先考慮遺傳複雜的綜合性狀，數量性狀。儘可能避免在數量性狀上的低劣類型作爲親本。

C.要優先考慮親本基因型

因爲果樹品種的基因型，目前瞭解尙少，一般在選擇親本時，主要是選擇優良的表現型(phenotype)。

(A).對一、二對基因控制的質量性狀，要研究育種資源是否具有我們需要的基因，是同質結合或是異質結合。

(B).對於數量性狀除要求表現型值不在中等水準以下，還需要研究不同育種資源之親和性。

D.應選擇育種値較大的性狀

多基因控制的數量性狀，性狀間遺傳力差異很大，如桃遺傳力較大的性狀有成熟期，果肉硬度(0.73～0.84)，遺傳力中等的有花期，花量和果形指數等(0.31～0.39)，遺傳力較低的有產量(0.08)。選擇親本時應著重考慮性狀育種値較大的品種作爲親本。

E.優先考慮一些少見的有利性狀和可貴的類型

如蘋果單基因控制遺傳的緊湊型，蘋果炭疽病及褐斑病等之免疫品種等均爲可貴的品種類型。又如桃品種中黃肉不溶質及豐產的品種也少且可貴。

5.雜交親本的選配

親本選配的原則：

(1).應儘可能使親本間優缺點互補。

(2).應考慮主要經濟性狀的遺傳規律。

(3).應選配在生態地理起源上相距遠的雙親

果樹雜交育種的親本選配，一方面要求親本在重要經濟性狀上的育種値高，也就是有較高的加性效應。另一方面親本選配上要求親緣關係較遠，至少用生態地理起源上距離較遠的不同品種類型雜交，以便在雜種中獲得較大的非加性效應。

(4).應考慮母本和父本在性狀遺傳下的差異

在親本選配中，爲了加强與細胞質基因有關的性狀的傳遞，應該把性狀表現優良的品種作爲母本或安排正反交對比試驗。

(5).應考慮品種繁殖器官的能育性和交配親和性

A.繁殖器官的能育性

(A).果樹中雌性繁殖器官不能正常受精或不能形成正常雜交種子者，不能作爲母本。如無子葡萄、無子蘋果、無子蜜柑等。

(B).雄性器官退化不能形成花粉者不能作爲父本。如上海水蜜桃、白桃、砂子早生等花藥萎縮不能產生正常花粉。

(C).雌雄器官均退化，或無融合生殖之品種。如蘋果屬中的錫金海棠、三葉海棠、湖北海棠，樹莓屬內的一些品種及鳳果等，種子一般由珠心細胞不經受精發育而成，不能作爲雜交親本。

B.交配親和性

自交結實率低的種類，如梨、甜櫻桃，等出現品種間雜交不親和現象，尤其是遠緣品種間此現象更爲普遍。如：

(A).正反交不親和：菊水(廿世紀 × 太白)和廿世紀，衹園(廿世紀 ×長十郎)間存在之雜交 不親和現象。

(B).正反親和、反交不親和: 如李品種間雜交。

6.雜 交

(1).雜交前的準備

A.制訂育種計畫

雜交育種計畫應包括育種目標，雜交親本的選配、雜交後代的估計、雜交組合數、雜交花數、雜交過程(如花粉採集和雜交日期)、操作規程 (雜交用結果枝與花朵選擇標準、去雄、花粉採集和處理、授粉技術要求等)、以及記載表格。

B.熟悉花器構造和開花習性

(A).花器的類型分爲兩性花和單性花，兩性花中應瞭解雄蕊和花柱是否等長、雄蕊的數目、花粉量、以及雌蕊的胚珠數。

(B).開花習性

a.因不同的種和品種而異。

b.環境條件也影響開花早晚和花期長短。

c.花序之花朵開放順序不同，如蘋果是離心開而梨爲向心開。

d.雌雄異熟現象，如番荔枝科中之刺番荔枝、冷子番荔枝等。

e.某些花比另一些花著果率高。

f.開花受精

在自交能結實的品種中，有的在花朵未開放前就可授粉如葡萄。

C.準備雜交工具

雜交時的用具有: 去雄用的鑷子、貯粉瓶、乾燥劑、授粉器、塑膠牌、擴大鏡、鉛筆、70%酒精、紙袋和縛扎材料等。

(2).雜交的步驟和方法

A.花粉的採集和貯藏

(A).花粉的採集：通常在授粉前，從父本植株上採集即將開放的、發育好的花蕾或花序，在室內挑取花藥，一般在室溫條件下，讓花藥開裂，散出的花粉收集小瓶中，貼上品種名，立即置於盛有乾燥劑($CaCl_2$)的乾燥器內。

(B).花粉的貯藏：通常在黑暗、乾燥、低溫的條件下貯藏。溫度0～5℃左右，相對濕度不高於30%，果樹花粉的壽命因品種和貯藏條件而異。

a.蘋果、梨、桃、柑桔的花粉，在室溫下可保存2～5週；葡萄、枇杷有兩個月；柿的

花粉只能保持兩天的活力。

b.桃和梨的花粉在0～2℃，RH25%下，可保存1～2年。

c.一些熱帶、亞熱帶果樹，如荔枝、鳳梨等，花粉活力保存期短，最好隨採隨用。

B.母本樹和花朵的選擇

(A).母本樹的選擇：選品種正確，生長健壯，開花結實正常的優良株。

(B).雜交用花朵的選擇：選著果可靠部位、側枝生長健壯，結果母枝粗壯，結果枝生長良好、花芽飽滿。蘋果中心花著果率高，梨則邊花著果率高，柑桔以有葉單頂花著果率高。

C.去雄和隔離

(A).去雄：為防止兩性花品種自交，在花蕾長大，花藥成熟開裂之前去雄。

(B).隔離：去雄後立即套袋以防止天然雜交。

D.授粉和掛牌

(A).授粉：去雄後柱頭出現黏液時，表示雌蕊成熟，此時授粉的結實率最高。如在大蕾期去雄後立即授粉，也能獲得高結實率。花粉用量多，結實率亦高，種子也多。多次授粉也有較好效果。

(B).掛牌：授粉後立即套袋隔離，掛上塑膠牌寫上雜交親本和授粉日期。

(3).雜交果實採收和種子處理

A.雜交果實採收

(A).授粉後，雌蕊枯萎時即可除去隔離袋，使幼果生長發育良好，生理落果期後套上網袋防止採前落果。

(B).對母本樹應加强管理、合理施肥、防止病蟲害、疏掉一些非雜交的果實。

(C).為使種子能充分成熟，雜交果實宜適當遲採。果實採收後，應放在冷涼場所讓種子後熟，以提高種子活力。

(D).早熟品種應延遲採收或在果實採收後延長果實成熟期。

B.種子處理

(A).早熟品種如桃早熟種，採收後及時取出種胚即行培養。敗育的種胚，早採收，行胚培養可提高雜交後代的株數。

(B).具休眠性之種子自果實中取出後，沖洗乾淨後，用殺菌劑處理種子表面，再以2～5℃行濕冷層積打破其休眠。

(C).常綠果樹，如柑桔、枇杷、荔枝、和龍眼等種子不易保藏，取出種子洗淨、滅菌處理、晾乾後即予播種。

(4).提高雜交率之途徑

A.提高雜交受精可能性

(A).利用雌蕊不同年齡時期授粉。

(B).採用正反雜交。

(C).調節親本花期。

a.延遲開花的方法

(a).樹冠覆蓋遮蔭，以降低溫度。

(b).延遲修剪時期，早春才修剪。

(c).嫁接結果枝。

(d).噴施生長調節劑，早春噴施 K-NAA 250～500ppm。

(e).將盆栽樹種置於冷涼地方。

b.促進開花方法

(a).將有飽滿花芽的枝條，在溫水中浸12～24小時，然後揷入5～10%的蔗糖溶液內，放置在溫暖濕潤的溫室中。

(b).植株盆栽後，於早春放入溫室內。

(c).對蘋果等有休眠性之果樹，提早低溫處理，加速花芽之休眠過程而後在常溫下，可以加速開花。

(d).高接已打破芽體休眠之帶花芽枝條。如台灣地區目前採用之嫁接梨生產技術。

(D).花粉貯藏

雜交父母本花期相差太長，可在前一年採集花粉置低溫下貯藏到第二年供授粉用，本省落葉果樹中梨之雜交育種，在平地授粉即採用花粉貯藏。

B.提高雜交結實率和種子數

(A).提高雜交結果實率之措施

a.選通風、光照條件良好、生長健壯無病蟲之母本樹。

b.取健壯的結果母枝或結果枝上發育良好之花朵供雜交用。

c.適當疏除其他非雜交之花朵及果實。

d.進行去雄、授粉、套袋等操作時，避免損傷花朵和花梗。

e.兩品種間雜交時，儘量選用結實率高的品種爲母本。

f.加強授粉著果後之管理作業，避免因缺水、缺肥及病蟲爲害所造成之落果。

(B).提高雜交種子數之措施

a.授粉時採用有活力之花粉，必要時行兩次授粉。

b.選用發育良好之花朵，母本子房內的胚珠發育良好，並能產生活力的配子。

c.如用不同成熟期品種間雜交，原則上用成熟期較晚的品種當母本。

C.提高雜交工作效率

提高工作效率之措施

(A).自交不親和的果樹，行不去雄的雜交。

(B).在大蕾期授粉。

(C).用化學方法去雄。

(D).採用去花冠去雄法，便於操作且不套袋。

(E).用稀釋的花粉，節省花粉用量。

(F).利用尼龍紗罩覆蓋整株雜交母本防止天然雜交，來代替對每一朵雜交花的套袋手續。

7.雜種的培育

(1).培育雜種的基本原則

A.提高雜種實生苗的成苗率。

B.培育條件均勻一致。

C.根據雜種性狀發育的規律進行培育。

D.有利於實生苗提早結果。

(2).培育雜種的方法

在整個培育過程中，應該提供雜種良好的培育條件，使其生長發育良好，充分表現性狀特性並提早結果。

A.播種育苗

爲使雜種提早結果，可以提早育苗。沒有明顯休眠期的樹種，果實採收後立即播種。有休眠期的落葉果樹類，一般需要在2～5℃潮濕之介質中層積打破休眠後才能發芽。同樣可在果實採收後即予處理催芽。

爲使幼苗能夠生長迅速而健壯，要注意光照、通風、施肥和澆水、以及防治病蟲害。

B.幼苗移植

爲便於管理及促進幼苗生育，可移植於塑膠袋或素燒盆，在苗圃中集中培育。

C.苗木管理

對雜種實生苗，除給予充足的營養和水分外，應特別注意病蟲害防治，培育健壯之實生苗。

D.實生苗定植

爲使雜種實生苗快速生長，宜儘早將苗木定植於育種果園。定植前可先行早期選拔淘汰。

在育種果園內，應該根據雜種正常生長結果和操作管理方便所需之最低程度的營養面積安排定植距離。通常可採用寬行密植之原則。定植時植穴要深，施入足量之基肥，帶土移植儘量減少根系損傷。

定植後應採取縮短幼年期，促使雜種提早結果的有效措施，加强培育管理。

(3).果樹實生苗的幼年期

A.幼年期的概念

(A).所謂幼年期(juvenile period)，就是指從種子萌發到實生苗具有正常開花潛能之一段時期。

(B).從實生苗到開花結果，可分爲三個時期，即幼年期、轉換期(transition period)及成年期。實生樹的階段性分區如圖3所示：

(C).縮短幼年期的不同見解

a.Fritzsche (1948)等人認爲幼年期是不能縮短的，它受遺傳控制，有一定的發育程序，實生苗提早開花是由於縮短轉變期，而不是縮短幼年期。

b.Zimmerman (1972)認爲只有當實生苗處于轉換期時應用生長調節劑等措施才可以提早開花。圖4.

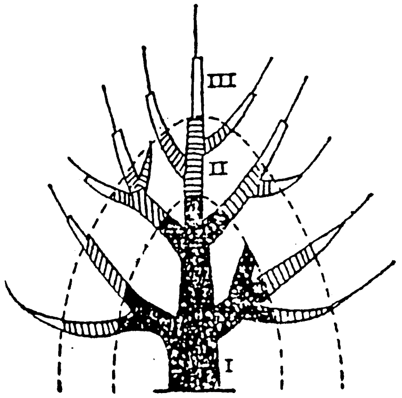


圖3. 實生樹的發育階段性分區(蘋果)

Ⅰ、幼年區。 Ⅱ、轉變區。 Ⅲ、結果區。

(Passecker, 1949)

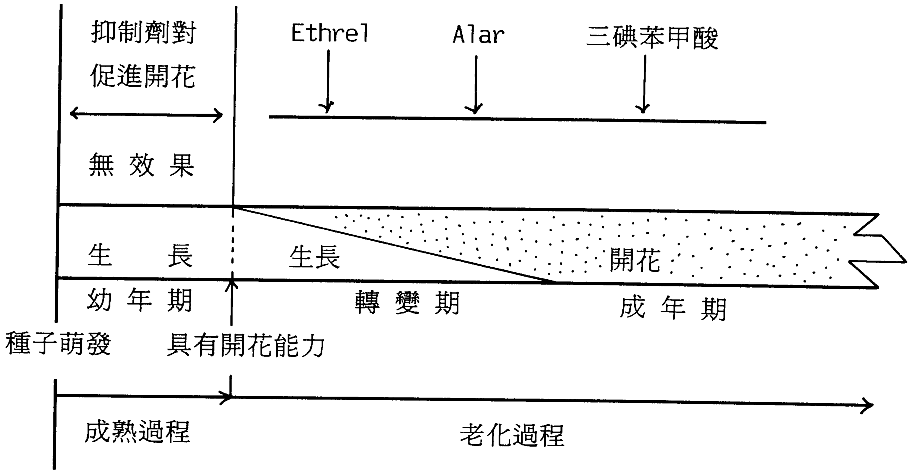


圖4. 實生樹的發育階段和開花反應

c. Passecker (1952), Wellensick (1952)等則認爲幼年期是可以縮短的。並且認爲凡是促進營養生長的措施都有可能縮短幼年期。因此，只要爲實生苗創造一定的環境條件和生理條件，就能顯著加速實生苗的生長發育，明顯地超過常規栽培措施所能取得的提早開花效果。環境影響縮短幼年期是由於增加實生苗的生長量和營養物質的貯備，以及有關激素的產生和達到激素的平衡從而引起開花基因的活化，使在生理上提早達到成熟。

B.幼年性

幼年性是指某樹實生苗幼年期階段所表現的形態特徵，解剖結構和生理特性。

(A).形態特徵

a.葉片：實生苗幼年期的葉片通常較小，隨著生長年齡而增大，葉片趨向定型時，表示幼年期結束。幼年期葉片，有些樹類之葉緣呈銳鋸齒狀而後向鈍鋸齒狀特化。又如葡萄及麵包樹實生苗葉片，早期裂刻較深，後變淺。

b.芽：幼年期的枝條中部和上部多數爲較飽滿的葉芽，下部多發育不全而質量較差的盲芽。

c.枝條：幼年期的頂芽生長旺盛，加高生長明顯，枝條有位置效應，主枝有明顯的生長優勢，生長在直立莖幹上的枝條隨著結果年齡的到來而趨向於平展，而且隨分枝級數的增加而減少，幼齡樹有多次抽梢習性，隨年齡增加而減弱。且枝條頂端相對較細，不很充實，隨年齡增大而增粗，尖削度逐漸減少。

d.針刺：柑桔、蘋果、梨、棗等的幼年期實生苗常有刺。

(B).幼年期的組織結構特徵

a.葉：Ware (1959) 發現幼年期實生苗的葉肉發育差，柵狀組織和葉脈不發達。表皮細胞大，單位面積內氣孔數少。

b.枝：F. Kobel發現蘋果幼年期葉片和枝條的結構特徵如表2.所示。

表2. 蘋果幼年期枝、葉組織結構的差異

性狀 ＼ 發育時期	葉片				枝條			
	葉肉	葉脈	柵狀組織	單位面積氣孔數	一年生枝橫切面木質部比例	木質部纖維素	導管數	薄壁細胞
幼年期	不發達	不發達	不發達	少	高	多	少	少
成年期	發達	發達	發達	多	低	少	多	多

(C).幼年期的生理特性

主要表現在生化成分、光合作用的功能、細胞液濃度、物質代謝、酵素的活性、激素的種類含量和平衡、以及生根能力等方面。

a.成年期枝上還原糖、澱粉、蛋白質、果膠物質都比幼年期多。C/N 比率較高，生長點分生組織處於活躍狀態，而且細胞液濃較高的條件下，有利於花芽形成(Fritzshe, 1952)。

b.Luckwill (1970) 指出果樹幼年期的迅速生長是由於內源 GA 含量較高，而成年期則含有較高的 Cytokinin。Cytokinin 含量高有利於花芽分化。

c.幼年性的枝條具有易於形成根的能力。

d.蘋果和柑桔幼年期階段實生苗的葉片組織中 RNA 含量低，RNA 酵素活性強。

C.幼年期的長短

(A).幼年期的長短因種屬不同而有顯著不同，大致可分爲四個類型：

a.長幼年期類：一般在9-10年以上，如銀杏、楊梅。

b.較長幼年期類：一般在7-9年之間，如柑桔、核桃、柿、栗。

c.較短幼年期類：一般在5-8年，如蘋果、梨。

d.短幼年期類：一般在3-4年左右，如桃、李、杏、棗和葡萄。

(B).影響幼年期長短的因素：

a.親本的基因型。

b.雜種培育條件。

c.親本營養期的長短：親本營養期短，後代幼年期短。

d.樹種的生長習性：灌木比喬木的幼年期短。同種果樹中矮生型品種比喬化型的幼年期短。

e.其他生育特性：一般頂端優勢較弱，幹性不明顯分枝角度大，側枝生長好，樹冠比較堅湊，節間較短粗，枝頂較粗大，針枝易于演化短枝的樹種和品種，大都能較早地形成花芽和提早結果。

D.果樹實生苗提早結果的途徑和方法

(A).選擇早實性强的品種當雜交親本。

(B).選擇利用和人爲創造培育雜種的良好環境。

a.選擇培育雜種的良好自然環境條件，主要包括溫度、濕度、光照、土壤及地勢等。

b.利用溫室或人工氣象室培育雜種。

(C).採用合理的農業技術措施

a.適當的栽植距離。

b.提早播種育苗。

c.減少移植次數。

d.良好的營養條件。

e.修剪和枝條處理。

f.環狀剝皮。

g.高接。

h.利用矮化砧。

i.應用生長調節劑：GA、Alar、CCC、Ethrel。

j.綜合的果樹栽培技術措施：提高栽培管理技術，促使實生苗生長健壯，儘快達到開花結果所需之臨界高度，並形成大量有效葉系上述之途徑與方法可以圖5簡明表示。

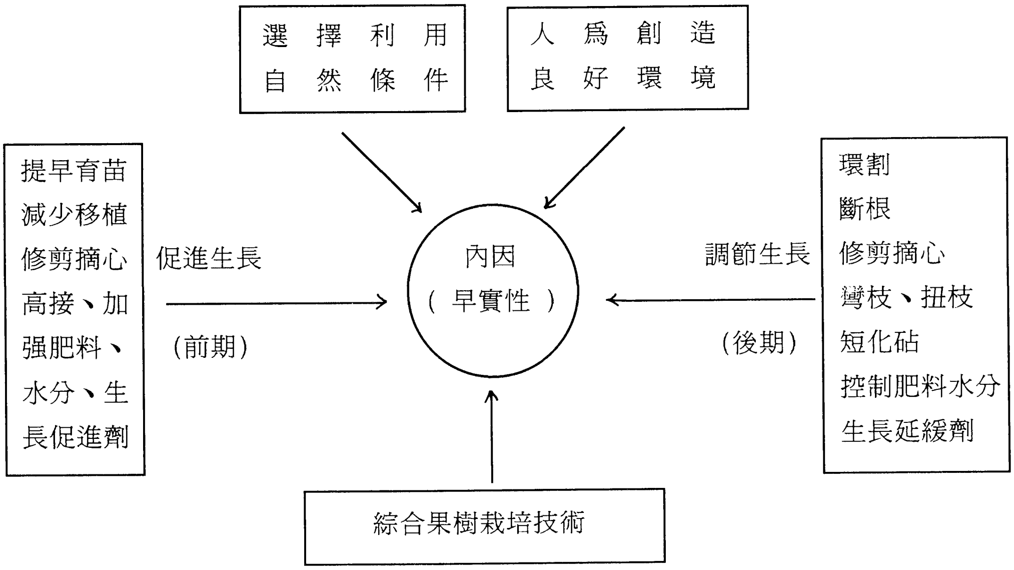


圖5. 果樹雜種實生苗提早結果的途徑

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果樹育種策略及台灣果樹育種常見之問題

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果樹育種方法之使用及效率之增進

一、前 言

育種主要爲選拔具有優良特性之植株，加以繁殖，並於適合環境進行評估後命名推廣，再以獲選優良植株爲親本，進行雜交或以其他育種方法，重複此一過程，果樹不同於其他作物，其涵蓋範圍極廣，從草本之鳳梨、木瓜，藤本之百香果、葡萄，以至木本之梨、芒果均屬之，所使用之育種方式亦不相同，以下列數種作物爲例，因應其特性採用不同育種方法，但均能達到獲得優良品種之要求。

1.酪梨、芒果等之自然授粉實生選種：仍爲許多果樹重要品種之主要來源，酪梨於公元前 4,000 年即似有選種之跡象，但至20世紀之今日，主要栽培品種如 Fuerte, Hass, Lula 等均爲自然授粉實生苗中選出；芒果亦然，Haden, Irwin, Tommy, Atkins 均爲佛羅里達由自然授粉實生苗中選出。

2.藍莓之馴化及雜交育種：爲本世紀才馴化及育種成功而有經濟栽培之果樹， 1906 年美國 Dr. Coville 首先進行育種，1921 年育成 2 品種首次採收以至於今之不同品種。

3.加州草莓之種間雜交，育成日中性品種：採用回交育種法，於三個世代之時間即將野生種之日中性轉移至栽培種，果重由野生種之 2 公克增至栽培種之 20 公克。

大部分果樹爲由高度異質組成之族群，幼年期長使育種時間較長，植株體積大型常需較大面積及投入，因此使育種之成本較高，但果樹可經由選拔優良單株無性繁殖而迅速固定優良遺傳組合，此爲其他糧食作物或種子繁殖作物所不易達成者。由於優良品種常用以爲親本，因此，許多重要果樹品種之來源往往可溯自單一品種，本省芒果主要品種多爲早期自美國佛羅里達引進，其中 4 品種 Haden，Irwin，Keitt，Zill 均爲自 Mulgoba 之實生苗中選出；美國柑橘栽培品種亦有此一現象，大部分甜橙重要栽培品種只有微小基因之差異，而葡萄柚爲美國第二大柑橘，主要品種多來自 Duncan 及其衍生之 Marsh。檸檬之品種亦多來自 Eureka 及 Lisbon ，只有寬皮柑之種源較廣。育種之原則爲自大族群或基因庫中選擇優良品系，如果此類優良單株或品種經常用以親本，將無可避免造成基因庫日異狹窄，由此類品種構成之族群如用於自然授粉選拔，其基因重組及變異程度將遠比來自不同種源之品種組成之族群爲低。近年來，育種多主張於異交作物採用混合選種或輪迴選種法，不但可達到育種目標，且不致遺失其他重要因子，果樹雖世代較長，且植株高大，未必能完成配合使用，其原理則一，如選擇親本不考慮及此，將事倍而功半，此點

臺大蔣明南教授已有詳盡之說明。

二、果樹育種常遭遇之問題

(一)經費及人力不足無法達成預定目標：

經費不足常造成：

1.無法獲得足夠種源。

2.無法培育大量族群供選拔。

3.無法進行適當規模之育種技術：如人工雜交之人力，評估育種之設備及經費。

4.常以短期可達成目標代替需長期才能完成之目標。

5.無法充分評估品系，於命名前不能充分了解其特性。

同時，應配合產業之需求而決定育種之規模及計畫，栽培面積少而進行大規模之育種計畫爲不切實際。

(二)育種方法之使用，果樹爲長期作物， 自育種之開始至發現錯誤可能已浪費 5～15 年之時間，因此，育種尤需注意方法之使用。

常見之問題爲：

1.於狹窄之種源或基因庫中進行育種，不易達成目標，如本省桃育種初次進行時採用低海拔鶯歌桃與高山桃進行雜交均失敗，無法獲得種子，後至美國佛羅里達州等地引進低需冷性桃取代本省鶯歌桃爲親本，才獲得雜交成功，據推斷美國已進行低需冷性及高需冷性桃之雜交，且獲得相當數量之品種，其遺傳成分經不斷重組，與高需冷性桃之雜交親和性較佳。

2.不了解作物之授粉模式：授粉模式及著果率決定育種方法及雜交授粉技術之採用，常見之例爲：

(1) 因授粉困難而決定以自然授粉取代人工雜交授粉，但未注意此果樹爲自交親和，且自然授粉（無論自交或雜交）無法達到希望之基因重組，造成育種投資之浪費。

(2) 著果率決定人工雜交授粉之可行性，澳洲胡桃以人工雜交授粉所獲得之果數極少，造成可供選拔之族群極小，其選拔效果往往不如由自然授粉獲得之大量實生苗。印度雖然進行許多芒果品種間雜交，但目前世界主要之芒果品種仍多爲自然授粉實生苗選出者，主要之原因亦爲人工雜交之結果率極低，最近採用改良之雜交技術才稍克服此一問題。

(3) 胚型決定親本之選擇及育種方法，多胚性於果樹中極爲常見，自多胚性之果樹之實生苗中選種效率較低，柑橘育種以多胚性爲母本，須先能鑑別無性胚及有性胚，並除去無性胚之實生苗；芒果育種以在來種爲母本是自找麻煩，於芒果實生苗中選拔效果近於零。

3.採用錯誤之育種方法，浪費人力而無效果，例如：

(1) 於變異極低之果樹種類進行實生選種。

(2) 新興果樹或栽培面積小之果樹應先以引種或選種，再逐步進行其他育種方法，引種應注意引種地區及氣候。本省芒果之栽培由無到今日之一萬六千餘公頃，主要之品種仍

爲佛羅里達引進之愛文、海頓、凱特及聖心等，自東南亞或印度引進之芒果品種多結果不良，可能其對開花期之低溫較佛羅里達品種敏感。

(三)育種目標輕重不分：

(1) 病蟲害如藥劑極易防治，不應以抗病蟲害爲目標。

(2) 目標太高，於現有果樹種源（基因庫）中無法找到親本，其目標不易達成或即使達到亦影響其他性狀之表現。

(四)育種程序之誤失：

(1) 應自代表性族群或植株取樣，且只調查有需要之數據，而族群之數目應足以使選拔性狀分離。

(2) 不必每次自優良性狀之原始親本獲得因子，否則可能太費人工及經費。

(3) 選擇適當親本，親本應隨世代推移，勿於雜交數代之後仍用同一親本。

(4) 依據育種目標擬訂性狀選拔之優先順序勇於淘汰不良品系，大部分果實性狀（除產量外）可在 1～3 年內確定。

(五)應盡可能了解新品種之栽培方法及特性，如與不同砧木之親和性、抗病蟲害、肥料施用等，以免造成日後之困擾。

三、果樹育種效率之增進

果樹育種最主要之障礙有二：1.植株體積高大（與農藝作物或蔬菜、花卉等比較），需投入較高之成本及土地，常造成評估株數不足，無法選出優良品系，Hansche (1983)比較草莓與桃育種之成效，發現草莓育種於過去15年可使產量從每公頃15噸增加至 100 噸，但桃育種於產量則無明顯之增加，由遺傳率之估算認爲其原因乃由於評估株數較少，而不易於產量選拔得到效果，因此，植株樹體高大之作物，縮小或矮化植株後，增加供選株數遠比複雜之育種方法更能有效的改善育種效率。2.長幼年期使每世代所需時間延長，造成低育種效率，如某一性狀每世代可改善15％，幼年期 5 年之果樹，將使育種效率降爲每年 3％ 以下。因此改善果樹育種效率須先從此著手，包括：

(一)高密度種植實生苗，可大量增加供選拔族群。

(二)促進雜交後代之早日開花結果，包括：

(1) 選擇幼年期短之品種爲親本，如東方梨、荔枝之沙坑種。

(2) 高接。

(3) 化學藥劑使用。

(三)正確之育種方法及技術：

1.依變異之來源及程度決定育種方法及親本，適時調整育種方法以達成目標：

蘋果之 Crawley Beauty 及 McIntosh 遺傳大部分性狀至其後代，而 Cox's Orange Pippin 之實生苗變異極大；荔枝沙坑種之實生苗變異亦大於黑葉種； 柑桔之葡萄柚與寬皮柑亦產生許多極重要之栽培品種，大部分有潛力之品種親本均來自種間雜交之 F_1 ，其中超過1/8曾以葡萄柚爲親本。

2.依授粉模式決定育種方法及雜交技術：

(1) 於荔枝、酪梨等，可利用雌雄花之時差自然授粉而獲得雜交率高之種子。

(2) 以自然授粉取代部分人工雜交，利用自交不親和品種，或以混合品種花粉代替單一品種，芒果高接自交不親和之不同品種代替人工雜交。

(四)苗期篩選：

1.於幼年期先除去具有不利性狀之實生苗，例如抗病蟲性、耐寒性。

2.以相關性高之性狀於幼年期先行評估。

四、結論

1.理想之品種幾乎不可能達成，而理想之性狀亦因時間而改變。

2.發展矮性品種為無可避免之趨勢。

3.避免錯誤之策略、程序及目標。

4.配合科學進展而改進育種方法及技術。

砧木育種

砧木育種為果樹育種所特有之項目，砧木影響植株之生育、果實產量、品質，並提供對環境之適應性，如抗病蟲、耐旱、不良土壤條件。果樹育種家往往針對其環境及果樹之需要而發展其特有之砧木，如以色列針對其鹼性土壤而發展酪梨及芒果耐鹽砧木，美國針對酪梨之根腐病而有抗根腐病砧木，柑橘因寒害、毒素病及根腐病而改變原使用之砧木。

優良砧木之主要條件：

1.繁殖容易：無論經由種子或無性繁殖（利用多胚性或根插等)。

2.與栽培品種之嫁接親和性強。

3.對果樹植株、果實品質、產量有增進作用。

4.對環境之適應力及抗病蟲性強。

一、育種目標

1.矮化植株：指用於砧木或中間砧可限制植株生長，達到矮化效果，此於溫帶果樹已獲得重大進展，但於柑橘、芒果等常綠果樹則尚待發展。

2.產量：為最重要的目標之一，尤其對加工品種；產量及植株之大小無關，與著果率、果重有關，亦需評估對隔年結果之影響。

3.品質：幾乎與品質有關之因素均受砧木之影響，如果大小、果色、皮厚（柑橘等）、果汁量、甜度、酸度及營養成分（維生素及礦物質）等。

4.環境適應性：

(1) 耐寒性：柑橘枳殼較耐寒。

(2) 耐旱、耐濕。

(3) 土壤 pH 及不良土壤。

(4) 病蟲害：抗根腐病、毒素病、線蟲等。

二、砧木育種之困難

1.同時需評估園藝性狀及砧木性狀，評估抗病蟲性、耐鹽性可能只需數個月，通常於三年內可完成，但如評估園藝性狀需數年，甚至數十年之時間，而獲得之結果往往只適用於試驗地區，或使用之接穗，甚至只有其試驗之穗砧組合。

2.一再重複評估地上園藝性狀如產量、品質，對地下部分不易了解，易使研究人員漸而放棄。

3.自然發生之變異不如地上部之園藝性狀易於發現。

4.其成功與否比一般育種更受環境 － 遺傳之交感作用而影響，環境因子可能一夜之間使試驗植株完全受損，如颱風、低溫等，佛羅里達二年大寒低於零度以下，使北部柑橘完全凍死，試驗植株全毀。

三、本省砧木育種之可能方向

1.柑橘 － 適合本省商業品種之砧木及穗砧組合，包括抗病蟲砧木。

2.芒果矮性砧木發展。

3.酪梨耐根腐病砧木之引進及試驗。

4.其他根部病害：如龍眼、百香果等之抗病砧木。

品系選拔、試作及評估

果樹品種自雜交授粉、品系或變異選拔以至品種命名，所需時間因作物種類、育種目標及育種方法而異，短者數年，長者數十年，但其主要育種程序大致相同。美國農部於佛羅里達 Orlando 之柑橘試驗所的 Dr. Hearn 曾比較柑橘育種時間因時地而異，1904 年佛羅里達桔柚品種 Sampson，自雜交授粉至命名只有之七年的時間，但1979年命名之寬皮柑 Sunburst，則花了十八年的時間，隨著品種之增加，育種目標之改變，統計方法之使用，所需評估之時間逐漸增長，亦表示要超越以往之優良品種，亦較爲困難，而品系選拔，試作評估方式之正確與否爲決定育種成敗之最大因素。

一、品系試作評估之原則

(一)公正及正確性：並做整體之考慮，勿因某品系，某些性狀表現特出而忽視其他缺點之浮現，配合統計方法之使用以評估各性狀 。

(二)應以主要栽培品種爲對照，對照品種之選擇依成熟期(早、中、晚)、地區、年份及育種目標而異。最好包含其他地區或其他國家之優良品系或品種，如此可：

(1) 與其他育種者之成績相比較。

(2) 提供世界性比較之基礎。

(3) 提供其他地區了解供試品系於其他地區之潛能。

(三)試作地區及栽培方法之選擇

1.試作地區之範圍、地點，應以品種主要推廣地或作物主要栽培地而定，以了解新品系之

地區適應性，如芒果於南部選出者應於中部地區試作，因開花期之溫度對產量有極大之影響，溫帶果樹之桃、梨於不同海拔之試作可了解其需冷性。

2.盡量以不同栽培方式、不同砧木（如因地區而不同），不同土壤環境多地區之試作，以期了解新品系之特性，但此種栽培環境與各地區農民之栽培環境相配合。苹果於乾熱季節著色不均，柑橘著色亦受地區溫度之影響。

3.對品系本身之了解而決定適當栽培方法，如耐蟲品系可施較少次或不施藥劑噴洒，以了解其抗蟲性，以避免影響其他益蟲之族群。品系是否爲自交親和而決定授粉品種之需要，自交親和品系產量較穩定且易評估，田間設計較簡單。

4.應充分了解環境因素對所評估果實特性可能造成之影響，如荔枝小核率常因品種或品系混植而降低，於商業栽培單一品種時小核率較高。

二、品系試作方法：因不同階段而異

1.實生品系選拔：目的在促使植株充分發育，早日達到開花結果樹形，以縮短幼年期，採高密度種植，於一定面積內可種植最多之實生品系，同時採用寬行密植，以利機械操作，間距可在 2至4公尺之間，株距0.25至1.5公尺之間，因作物而異，如爲長幼年期作物，以單行密植優於雙行密植，前者利於田間操作與調查，每株保留單幹至約1～1.5公尺高才分枝，以促使早日達到結果樹形，縮短幼年期。評估方式依育種家之經驗，並以各項儀器協助分析品質等性狀。

2.品系試驗（初級試驗）：目的在了解初選品系於現有栽培方法之表現，視需要而決定是否進行，由各地區已選出優良芽條變異或實生變異可先進行初級品系試驗，以採取多品系，較少重複或株數爲主，亦可嫁接於不同砧木了解其與砧木親和性及各種性狀之表現，應詳細調查各品系特性，栽培方式與栽培品種同。

3.地區試驗：其結果爲決定品系是否命名推廣之最主要依據，以適當數量之優選品系與對照品種組成，需多重複（4～6）及多地區進行，其調查項目應詳細並與以往結果比較以了解因地區而造成之差異，可因地區而採用不同砧木。

三、品系評估與選拔

評估性狀應先了解其遺傳方式，如爲質之遺傳，評估較易且於短時間即可確認，如爲量之遺傳，則需較長時間且配合統計方法之使用。果樹雖然自種植至開花時間較長，但據估計，除產量外各種性狀之遺傳率頗高，大部分之遺傳變方爲累加性，因此，以最簡單之混合選種法已足以有效之選出優良品系(Hansche，於 Moore & Janick(eds.)，1983)。因遺傳率不易估計，亦有復現率(repeatability) 估計廣義之遺傳率，如本省麻豆文旦之果實質地、果汁含糖量及風味三項復現率高，選拔效果大(李學勇等 1977) 。除產量外，通常三年已足夠評估各品系之表現，並加以選拔，選拔時間因育種目標而異，於幼苗期，可選拔性狀如無刺、抗病蟲性、耐寒性，於營養生長期，部分果樹可依葉色，而預估果色及果實生育期間等(Sherman & Lyrene，於 Moore & Janick(eds.),1983)，於果實成熟期選拔果實性狀，各種果樹性狀之遺傳應先參考前人文獻或本身之經驗，各果樹均有其特性，但亦有其相通之處，各種性狀之選拔方法如下：

(一)植株生育：

(1) 生長勢强弱：依株高、莖圍及經驗判定，生長勢强者爲佳。

(2) 植株矮化：可用砧木或矮性植株降低株高，植株本身爲矮性優於矮性砧木，矮性因子於果樹極爲普遍，例如桃爲一對隱性因子控制，矮性特性極爲明顯，誘變後亦極易選拔，須注意不可因矮化而降低產量及品質，芽誘變育種可於嫁接後 V1 期評估 (Lapins，於 Moore & Janick (eds.), 1983)。

(3) 幼年期短：於品種間變異極大， 爲累加性遺傳， 預估於李及苹果如選拔幼年期最短之10%植株，每世代應可縮短 10 至 14 個月之幼年期，選拔效果極大。

(二)開花期及成熟期：受年份之影響極大，但如以不同成熟期品種爲對照，可了解同一年份品系間之趨勢，因此，評估結果足以反應其遺傳特性。

(三)品質：評估項目極多，品系間差異大，其特性頗穩定，一般而言遺傳之表現大於環境影響，選拔效率高，評估原則：

1.年份之影響小於品系於品質之影響，第一次之評估結果與以後之評估差異不大，尤其對照品種之設立將使樹體，田區等環境之影響降至最低，大部分低於對照品種之品系於前二年即可淘汰，但部分果樹如柑橘，樹齡對品質影響極大，則需較多年之評估或高接於其他試區再評估。

2.注意採收期及後熟程度對品質之影響，如爲一年多熟之作物，應於最大量採收期評估，如爲一年一熟作物，應於適當成熟期評估，或依成熟程度分段評估。

3.育種者應以本身之經驗配合儀器之協助進行初次評估，亦可用酵素分析等生化方法，協助評估果肉質地、褐化等性狀，於地區試驗則可採用多人組成官能測驗，以了解市場接受性，大量樣品時，每次評估以在 4～5 性狀，1～2 個重複， 8～12 人組成爲佳，最好每人評估樣品20～24個以內。

評估項目：

1.果色：受低夜溫影響大，此種環境下色素含量，維生素 C 及酸含量均高； 如選出適應性廣之品系則較不受影響，苹果、葡萄、柑橘於冷涼地區著色較佳，但荔枝果色則較不受環境影響。

2.果肉質地：與成熟度有關，果肉軟、脆程度較少受環境影響，於荔枝、龍眼尤其明顯。

3.風味：與可溶性固形物、有機酸、維生素 C 等含量有關，糖酸比爲柑橘品質及成熟期之標準，小果因細胞小、密度大、通常較甜；易受灌溉、施肥、土壤及樹齡等影響。荔枝於成熟期酸度降低程度於品種間差異極大；葡萄柚以父輻射線誘變可產生低酸品系。

4.營養成分：果實維生素含量豐富，作物間差異極大，品種間亦有不同，遺傳因子爲決定維生素 C 含量之主要因素，亦受日照、樹體、位置等之影響。

5.酵素含量：Peroxidase 及 Polyphenoloxidase 含量可了解褐化之速度，Polygalacturonase， Pectinmethyesterase 及 Cellulase 可了解果肉軟化速度，初選不必測量，可直接由果實變色及軟化判斷，但在命名前最好了解。

(四)產量：受植株本身遺傳因子及栽培環境之交互影響，遺傳率低，不易選拔，常需多年份多地區試作，爲選拔之方便，常將產量依作物特性區分成不同之項目，如果重、開花數、著果率

、自交親和性等予以評估，但最後之評估仍應以產量本身為依據，例如：本省梨育種採用(1) 短果枝形成數，(2) 開花量及親和性，(3) 開花時有無遲延萌芽來評估產量。荔枝則以每穗結果數評估，百香果以自交親和性評估。除產量本身外，其他因素亦有利於產量之分析，包括：(1)隔年結果性，(2)抗病蟲性，(3)矮性程度 (適合密植)。

(五)病蟲害發生率：亦受環境之影響，應與植病及昆蟲專家配合評估。

(六)氣候因素造成之損害：可了解品系之適應性，如風害可了解枝條脆韌程度，寒害了解低溫耐性，浸水可了解品種或砧木之耐濕性。

(七)貯藏性及貯藏病害。

(八)自交親和性與授粉樹之需要。

四、美國佛羅里達寬皮柑 'Fallglo' 品種之育種及評估過程

1962年	Bower X Temple 雜交得 376 實生苗。
1972～73年	評估實生品系 2 年，選出 1-73-68。
1974年	繁殖苗木，嫁接於 6 種砧木，包括 Sour orange、Carrizo 及 Rusk citrange，Swingle citrumelo，Cleopatra mandarin 及 Rough lemon。
1975年	種於 Leesburg (包括 6 種砧木) 及 Lake wales (4 種砧木)二地區，12 重複，每單株為一重複。
1978～1984年	評估產量、品質 (甜，酸度) (分10月及11月二次採收)、加工特性 (果汁色、果肉率)、自交親和性、並調查不同砧木對品系之影響。
1987年	命名。

本省主要果樹之育種目標，方法及執行機關

本省果樹自民國 60 年代由臺大蔣明南教授於農委會之大力推動倡導，並以經費支持，始逐漸有系統的進行育種工作，其所研議之幾種果樹育種模式及目標，如鳳梨、柑橘、梨、桃，均有極優良之成績，也因育種工作之受到重視，研究人員及經費日益增加，而後，於本省重要果樹，如柑橘、芒果、梨、荔枝、鳳梨、桃、木瓜、百香果、番荔枝、草莓及稀有果樹種源保存，均有報告及檢討。本省主要作物之育種目標及方法如下：

一、柑橘類

(一) 一般柑橘 (嘉義分所)

目　　標：不同成熟期、多種類、高品質、豐產、耐病蟲害。

育種方法：

1.引種：自國外引種。

2.選種：自本省各地選出優良變異，如早生及矮生椪柑等。

3.雜交育種：

(1)橙類：以桶柑為母本與早熟(Hamlin)，中熟(Pineapple)，及晚熟 (Valencia)之

甜橙及其他柑橘類雜交。

(2)柚類：以麻豆文旦爲母本與早生柑橘如 Hamlin 及 Marrs early 等雜交。

（二）柑橘砧木（農試所）

目　　標：適合本省環境與本省栽培品種親和、矮性、抗病蟲害。

育種方法：

1.引種：國內外砧木品種。

2.雜交育種：主要砧木品種間或種間、屬間雜交。

（三）金柑（宜蘭農工專）

目　　標：大果、豐產、外觀佳、皮薄而甜、果肉甘、少種子。

育種方法：

1.地方品種變異調查及選拔。

2.自然授粉實生品系選種。

3.長實金柑及寧波金柑之種間雜交。

二、芒果（鳳山分所）

目　　標：果色鮮豔、大果、不同產期、豐產、纖維少、果肉率高、品質優、抗炭疽病、耐貯藏。

育種方法：

1.國外引種。

2.自然授粉實生品系選種。

3.品種間雜交。

三、梨　（農試所）

目　　標：適合低海拔、高品質、豐產、耐貯藏。

育種方法：

1.國外引種。

2.雜交育種：橫山梨與新世紀、廿世紀、幸水及長十郎等品種間雜交。

3.選出優良品系之自然授粉實生品系。

四、荔枝（嘉義分所）

目　　標：不同成熟期、高品質及高小核率、豐產、果色鮮豔。

育種方法：

1.國外引種。

2.本省優良變異品系選拔。

3.品種及種間人工雜交。

4.多品種自然授粉實生品系選拔。

五、蓮霧（鳳山分所）

目　　標：大果、高甜度、肉厚、質脆、不同顏色、豐產。

育種方法：

1.國內外引種。

2.本省優良變異選種。

3.品種間雜交。

六、龍眼（嘉義分所）

目　　標：大果、豐產、不同產期、小核、高品質、矮性。

育種方法：

1.國外引種（自泰國)。

2.本省優良品系選種及自然授粉實生品系選種。

3.品種間雜交育種。

七、葡萄（農試所）

目　　標：高產量、高品質、風味優、無子、不同產期、不同種類鮮食品種。

育種方法：

1.國外引種及引進品種評估。

2.品種間雜交。

八、桃　（農試所）

目　　標：低海拔種植、耐熱、高品質、大果、風味佳、果形優、果色佳、果肉多汁、不同產期、耐貯藏。

育種方法：

1.國外引進低需冷性品種。

2.優良品種及低需冷性品種自然授粉實生品系選拔。

3.人工雜交授粉：

(1) 本省在來種與高海拔水蜜桃雜交。

(2) 低需冷性與高需冷性桃品種間雜交。

(3) 低需冷性桃品種間雜交。

九、鳳梨（嘉義分所）

目　　標：植株矮、葉緣無刺、果型整齊、大果、高品質、抗病、耐旱之鮮食及加工品種。

育種方法：

1.國外引種。

2.開英種優良株系選拔。

3.品種間雜交。

十、香蕉（香蕉研究所）

目　　標：抗病（黃葉病)、豐產、矮性、果形佳、果串整齊、品質優。

育種方法：

1.國外引種。

2.自然變異選種：自本省各地及組織培養苗變異中選種。

十一、番石榴（鳳山分所）

目　　標：無子或少子、大果、高品質、高營養成份、豐產、抗立枯病。

育種方法：

1.國外引種。

2.雜交育種：(1)以泰國種與本省優良品種雜交以改進泰國種品質。

(2)以抗立枯病白拔與其他品種雜交以選抗病品種。

3.誘變育種：(1)以秋水仙素處理育成四倍體供育成三倍體之材料。

(2)以放射線處理種子後選種。

十二、木瓜（鳳山分所）

目　　標：豐產、高品質、矮性、早熟、抗病蟲害（以毒素病爲主）、耐貯藏。

育種方法：

1.國內外引種。

2.種間雜交及回交，以抗毒素病之 *C. lauriflora* X *C. papaya* 再回交 *C. papaya*，以胚培養克服種間雜交不親和。

3.品種間雜交及回交，以回交改良抗毒素病台農 5 號之品質。

十三、楊桃（鳳山分所）

目　　標：1.鮮食種：豐產、高品質、果形整齊、軟枝、抗病蟲害。

2.果汁加工種：果汁率高、豐產、抗病蟲害、檸檬酸高、果汁色澤優。

育種方法：

1.國外引種。

2.品種間自然授粉實生品系選種。

3.品種間雜交育種。

十四、柿（及甜柿）（農試所）

目　　標：高品質、不同產期、大果、耐貯藏、低海拔種植。

育種方法：

1.國外引進甜柿品種。

2.選種：本省早期馴化低海拔，甜柿品種選拔。

3.甜柿品種間雜交。

十五、釋迦及番荔枝屬果樹（台東場）

目　　標：豐產、高品質、裂果率低、果形整齊、不同產期、抗病蟲害。

育種方法：

1.引種：國外引進刺番荔枝品系。

2.選種：本省釋迦實生變異選種。

3.番荔枝屬種間雜交。

十六、酪梨（嘉義分所）

目　　標：高品質、豐產、不同產期、抗根腐病砧木。

育種方法：

1.國外引種，包括抗根腐病砧木。

2.自然授粉實生品系選種。

3.品種間雜交育種。

十七、百香果（鳳山分所）

目　　標：大果、高品質、豐產、抗毒素病。

育種方法：

1.國外引種。

2.種間雜交及回交黃百香果以提高品質及產量。

十八、印度棗（鳳山分所）

目　　標：高品質及風味優良、大果、豐產。

育種方法：

1.國外引種。

2.實生或芽條變異選種。

十九、獼猴桃（農試所）

目　　標：低海拔種植、高品質、豐產、大果。

育種方法：

1.國外引種。

2.本省野生獼猴桃選種。

3.品種間雜交育種。

二十、梅（農試所、台東場）

目　　標：大果、豐產、抗黑斑病、果肉率高、種子鈍形且小。

育種方法：

1.自然授粉實生品系選種（台東場）。

2.引種：國外引種　(農試所)。

二十一、稀有果樹種源保存及利用

溫帶果樹：農試所。

柑橘、熱帶及亞熱帶果樹：嘉義分所。

熱帶及亞熱帶果樹：鳳山分所。

目標：1.保存各類果樹品種。

　　2.開發新興果樹品種及利用性。

育種方法：

1.國內外引種及評估。

2.引進種子等實生品系評估。

幾種果樹育種實例

一、鳳梨營養系選拔及雜交育種：為台大蔣明南教授（1982b）建議於嘉義農試分所進行，包括:

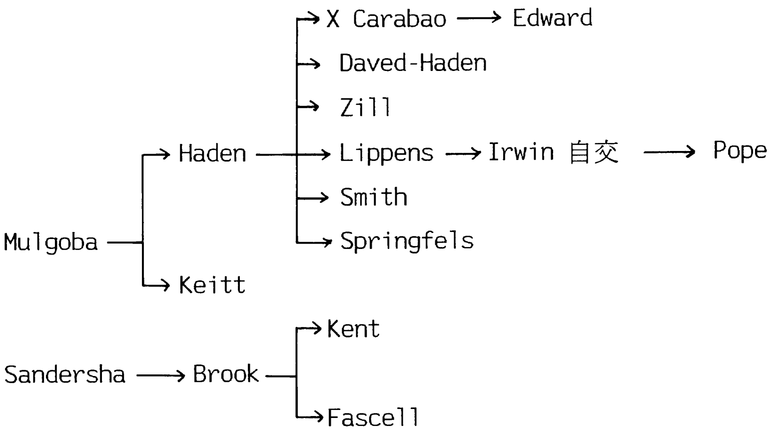
(1)營養系選拔：於主要栽培地區選拔具有優良性狀之營養系，每系約 2 至 5 株，再經數次複選，進行區域試驗而加以推廣。

(2)雜交育種：為避免傳統之品種間雜交造成優良基因不易結合於一之缺點，仍採用輪迴選種

法，以混合花粉代替單一品種花粉，而以兄妹交代替自交之方法，以促成優良基因之充分重組，並於其中選出優良單株，並改進族群優良基因之比率，目前已有優良品系之選出。

二、木瓜雜交育種：多採用品種間雜交或回交，再純化育成自交系，以鳳山分所台農五號之育成為例 (王德男等 1987)：民國 66 年由美國佛州引進耐輪點毒素病之 FL-77-5，選出紅莖及綠莖二優良系統，分別與 Costa Rica 雜交，分別自交 3～4 代，選出 4-4 及 34-3，再雜交後，選出自交系 85-3，並進行區域試驗而命名。

三、芒果自然授粉實生選種 ： 本省芒果主要品種多為美國佛羅里達引進，其中 Haden, Irwin, Keitt, Zill 均為自 Mulgoba 之實生苗中選出，其品種來源大致如下： 箭頭表示後代之產生，如 Irwin (愛文) 為自 Lippens 實生苗選出，而 Lippens 源自 Haden (海頓)，Haden 又來自 Mulgoba。



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花卉育種概論

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前言

花是植物具有雌雄器官的部位，也是花卉園藝上主要觀賞其變化的部位。現代的花卉園藝是農業的一部門，是計量作物，也可以計算投入的成本、產量和價格。但消費的形態與稻米等糧食作物完全不同，也跟其他園藝作物，如果樹、蔬菜等食用作物不同。所以育種的基本觀念，目標也跟其他作物差異很大，標準也不同。因此要有另立標準來評估育種成效的必要。

1.花卉消費的形態

在花卉園藝上栽培的作物，雖然可以用單位面積的產量，投入的勞力和資本，如肥料、農藥、資材等的多寡來計算成本和收益。但所具的價值和產生的效果，又常無法用客觀的標準來評估。如都市的花壇，所用花苗可用購買的單價來計算成本，但對市民的精神，心理所產生的效果，則無法計量。

由於花卉是視覺消費的產品，與繪畫、雕刻等美術品相似，與電影、電視等微有不同，所以育種上的成效評估，仍需具有藝術修養和商品價值的觀點。

2.高性和矮性

花卉的種類，依用途不同，可分爲切花用的高性植株和盆花、花壇用的矮性植株品系，所需選拔條件也不同。切花用品種一般需要花型良好、花莖長、吸收性良好的特性。盆花、花壇用品種則注重矮化、花色鮮麗、花朵多、花期長、每朵花不必花型豐滿等條件。這些條件與糧食作物的育種目標有顯著的差距。

3.種類，品種繁多，具流行性

凡是可供觀賞的植物，野生或栽培種，觀花或觀葉，都包括在花卉的範圍之內，所以種類很多。而每種的品種數，又因需求的不同，有更多的數量出現，且依時代的不同，社會形態的轉變，花色、花型、生態等均有不同的需求而產生流行性的改變。

4.繁殖形式不同，育種方式也異

如宿根類、球根類、花木類，均用無性繁殖法。所以雜交育種的後代，只要有一株優良的個體出現，就能成立爲營養系品種。用扦插、嫁接、分株、組織培養等無性繁殖法大量繁殖，推廣。但用種籽繁殖的一年生草花，則需用傳統方法，育成固定品種或F_1品種。

5.自然的芽條變異

由於花卉是欣賞植物外部形態的美，所以在自然情況下產生的芽條變異，只要能提高觀賞價

值的變化，都能選拔、分離、固定、成爲新品種。用無性繁殖的品種，也常發生芽條變異。花卉品種形成的歷史都相當複雜，較其他作物易出現異變。經詳細比較選拔之後，形成新的系統品種。

6.斑葉品種

將葉片上產生斑紋變化，供爲觀賞重點，是花卉園藝的另一重要部門。其出現斑紋的原因，至今尙未瞭解，而出現的變化範圍又相當的廣。有些斑紋會固定不變的出現，有些出現後，又會消失。至今尙無法用人工方法，穩定誘導斑紋的出現。現有的斑紋品種，都是依靠自然的群落中選拔出來。

7.缺少正確的育種記載

由於大部分的花卉品種，都是依靠私人種苗公司或個人的趣味業餘家所育成。所以不僅種苗公司不會發表新品種的育種過程，個人育成的新品種，常有親本不詳的情形，都影響以後的育種工作的進展。

育　種　目　標

1.大花性

爲一般追求的育種目標，通常野生種的花朵都很小，變化少，花瓣構造較單純。以注重單朵花，色彩形狀的切花用品種，均注意花朵形狀的增大，並有花瓣豐滿的趨勢。如菊花、玫瑰、非洲菊、火鶴花、蘭花等。

2.多花性

通常爲花壇用、盆花用品種追求的目標，不僅花朵要多，開花能整齊同時開花，又需花期長。最近重要的切花種類，如香石竹、菊花、玫瑰都有新多花型的切花用品種，這些不僅枝條長，每枝上都有10朵左右的花。

3.新花色

花卉育種中，這是很重要的目標，惟現有花卉種類的花色，大都已經進步到相當高的程度，如要育出新的花色，需要利用野生種或較遠緣的交配，如屬間雜交等，在技術上較爲困難。像玫瑰花很多人都想育出天藍色玫瑰花，由於野生種沒有存在而無法實現。近年來的細胞融合法有可能提供這種希望。雙色花的出現，也是近年來的趨向。

4.重瓣性

多種花卉，爲使花朵更豐滿、更美、提高欣賞價值，而成爲自古以來的重要育種目標之一。在野生種中，以突變情形會出現重瓣花，但因結實困難，在自然狀態下，很難維持後代而消失。所以通常在栽培種才有重瓣，野生種以單瓣爲主。惟重瓣性在遺傳上以顯性居多。

5.特殊花型

這是單瓣和重瓣以外的不同花型。有些花瓣的周邊面積增加而產生花瓣緣波狀的情形。也有花瓣產生大小缺刻的情形，如鬱金香的品系，可稱特殊花型。金魚草以花朵形似金魚而得名，但近十多年來有花筒裂開，不似金魚的花型出現，一般稱爲蝴蝶花型，也是特殊花型。

6.開花習性

通常有早生、中生、晚生之分，也有四季開花性。如以早生和中生交配，其子代開花性在雙

親之間。近年來，由於市場之需求，有趨向育成四季開花品種或易受調節開花的品種。因生產者均希望在消費旺季時，能出售產品。

7.植株形狀

一般分爲直立高性、分枝矮性和蔓性品系。如金魚草有高性切花用和矮性花壇用，香豌豆也有蔓性和叢性。這些矮性株，在遺傳因子上，可能缺少製造 GA 的因子存在，故而產生矮化，以劣性遺傳的情形存在。

8.強勢生長性

爲生長勢强壯容易栽培，全群每株的株勢相似，常利用F_1的品種，在花壇品種群中最常見，如矮牽牛、非洲鳳仙花、金魚草、四季秋海棠、百日草、萬壽菊等，都有F_1品種。球根類中尙採用種子繁殖的種類，也有F_1的品種，如新鐵砲是台灣百合和鐵砲百合的雜交後代，大多以F_1品種出售。生長旺盛，管理容易，是一般花卉育種所追求的目標之一。

9.芳香性

在野生的種類中，具有芳香的花卉不少，但在栽培品系中，具有芳香的卻不多。野生種的白花、黃花等及夜晚開放的種類，較具芳香，然一般育種大都注重色彩豔麗的花色，使新品種漸失去芳香。通常有芳香的花朵所含成分有 3～10 種之多，且以不同比例的濃度混合存在，形成每種花不同而有特殊的花香。依已往經驗，遺傳力不强。

10.斑紋品種

通常都靠自然的變異產生，雖可用放射線處理，但出現的機率不高，也不穩定。有體細胞的突變，也有遺傳因子的變化而產生。其出現斑紋的形狀、方式都無法預估或調節，所以一般都較稀奇。惟依常理，任何一種植物都會產生斑紋的葉，只是機率高低不同，形狀也各不相同。

育　種　方　法

依花卉的種類不同，育種目標不同，所採用的方法也各不相同。有時爲達到育種目標，將數種育種方法交替使用。育種方法不同，達到育種目標的年限也各不相同。

1.系統選拔法

又稱爲系統分離法，是育種上最早使用，最基本而有效的方法。花卉中有不少種類，品種數目少，尙在進化中的，常以混系的狀態存在，尤其種子繁殖的種類，形、色都不穩定。所以只要有確實的育種目標存在，都可以分離、固定、形成新的品種。當劣性的突變出現，如不即時選拔，給予保護，常會自然消失。所以系統選拔法雖然操作簡單，但需要敏銳的育種眼光和長期的努力。

2.種間、屬間雜交

由於單一原生種內所含遺傳因子的數量有限，爲擴大變化的範圍，以及引進優良的因子，達到育種目的，常進行不同種之間的交配。如蘭花常見屬間雜交。

3.F_1雜交育種

需先培育純系，並做試交，瞭解後代，才決定F_1品種的親本。爲降低人工授粉的操作，近年來出現不少自交不親和性、雄不孕性、純雌性等系統，並利用昆蟲授粉。

4.倍數體的利用

通常使用秋水仙精處理，創造人工四倍體。一般植株變粗大、葉片加厚、花瓣也較粗大。但生長較遲緩，易形成晚生種，且觀賞價值未必提高，有時只能當做交配親本。依據報告，四倍體較適合在溫暖的地域生長開花。

5.放射線的利用

經長年的研究結果，放射線處理雖能引誘芽條變異，但其變異的範圍只在遺傳因子的範圍之內，無法出現巨大的變異。所以放射線育種雖研究很多，但實際成效較少。

6.宿根類、球根類的育種

由於球根或宿根性種類都是用無性繁殖法來繁殖，形成營養系品種，所以在雜交後代的實生個體中，只要有一株優良個體，就能選拔出來，再經檢定比較，認定爲以往沒有的優良個體，即可經微體繁殖法，大量繁殖推廣。

7.細胞融合法

體細胞的融合現象，無血統間的關係存在，所以遠親的種間、屬間均能產生融合。如能在癒傷組織的增殖和再分化上的技術能突破，本方法是育成新品種最有希望的方法。將來也可能育出，這世界上已往沒存在過的新植物。

作物遺傳資源的保存及其利用
－概念與應用－

鄭崇成、黃永光
亞洲蔬菜研究發展中心

前　　言

『地球是目前人類所知的宇宙中，唯一能維持生命存在的地方，然而隨著人口的膨脹與須用的增加，人類對於這個行星的需索愈來愈大，而在此同時却因人類的行爲而使這個行星對生命的供給能力日減，由大多數貧窮者爲求生存的努力以及少數富裕而消耗了世界上大部分資源者，二者所結合的一個毀滅性的衝擊，正在逐漸損壞全體人類所賴以生存並昌盛的這一切財寶。』以上是國際自然保育聯盟在1980年的『世界保育計畫』中所提出的觀點，而植物遺傳資源的保存，正在這項挽救此危機之重要而迫切的工作上扮演了一個不可或缺的角色。

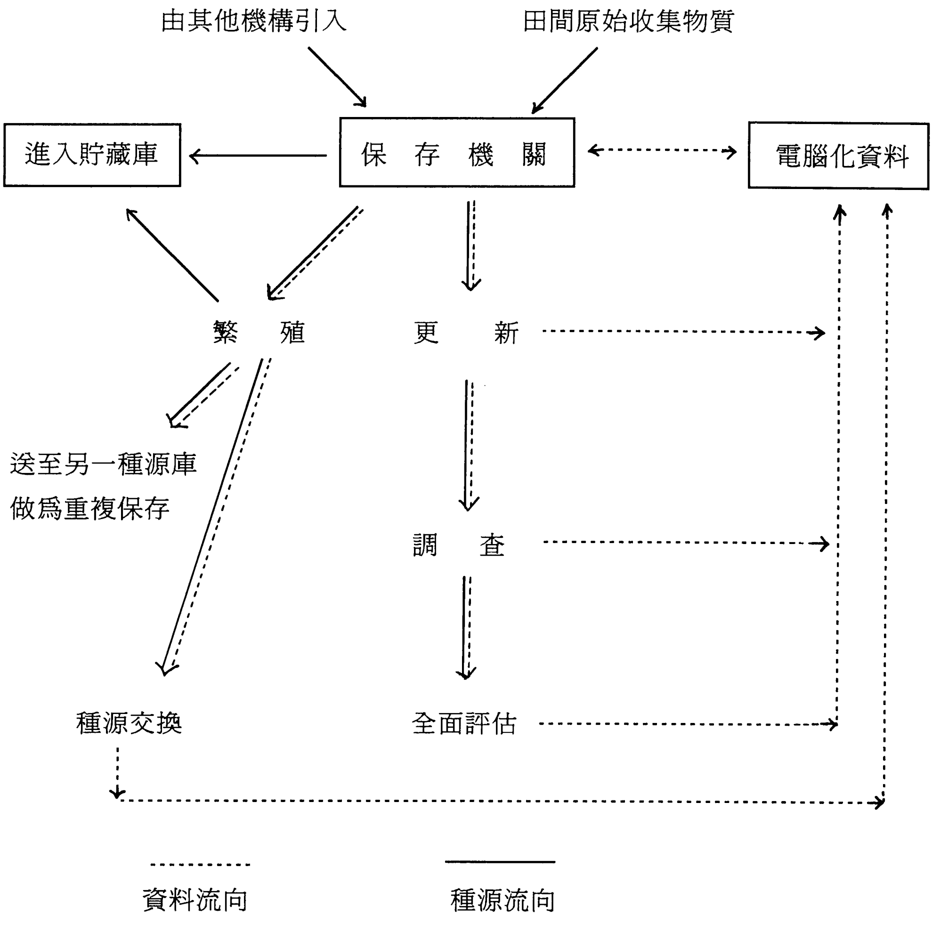
作物遺傳資源意指一個作物的所有品種所含有的一切遺傳物質，這裡面包涵了土生品種，因變異而具有特殊遺傳性狀的特定品種，作物的野生近緣種，流行好的或不好的栽培種，爲特殊目的育成的育成品種，過時的品種(如已不再被採用的品種)，一代雜交種等等。這些材料均能成爲作物改良的基礎。

不幸的是，就在過去的數十年間，在田野中上述許多有價值的種源，因爲下列原因喪失了：改良的栽培種的引入取代了產量較差的本地種；農業與都市的擴展如房屋與灌溉設施的建立，可能改變了自然的環境，如旱地或沼澤地等，以致剝奪了適應這些地方的植物種類之生存空間，這種情形下的遺傳物質的流失稱爲『遺傳侵蝕』，改良品種的引入不僅是由於其遺傳來源的狹小而製造了『遺傳弱點』，同時也是以很强烈的方式取代並消滅了其他較不受重視的作物，諷刺的是許多農業研究機構正以他們所改良合成的品種促成其他作物之多樣性的毀滅。因此目前最緊急的事就是必須去保存作物多樣性的完整。

植物遺傳資源的保存是一件極爲繁瑣的計畫，包含了探勘與收集，繁殖與保存，調查與評估，建檔以及最後的種源利用。這些不同事情的相互關聯以及其進行流程可以參見圖一。而各方面不同的知識在此被結合起來運作，舉例而言：植物種源的探勘與收集就要用上植物學、分類學、種的遺傳學知識，在採樣上須運用統計學以擬定採集計畫，而對於目標區之地理學及人種學上的了解能幫助行程的安排及人手的運用，最後還要爲所收集的變異定出其相異點的區別標準；至種子的繁殖工作上，則需要有關作物管理的常識以及該作物的育種方式才能繁殖出高品質的種子，而保存上則要明白種子生理學、組織培養技術以及冷凍保存技術以期能延長種源生命；調查工作則要求在植物分類學、生態學、解剖學、細胞學上有足夠的常識背景，另外化學分析技術如紅外

線光譜分析、電泳、染色體學等也會應用在此項工作上。由於種源最後必須被應用，所以育種的理論及方法也就是當然必須有的；生物技術則可以被用上基因轉移、鑑定重複以及研究品種間的血緣關係上。因此可以說植物遺傳資源的保存是一件與群策群力的工作，而每個工作成員在他自已崗位上的知識必須十分專精，並且對其他科目也要有大略的了解。

圖一、種源庫在處理種源上的一般程序



目前世界上主導植物種源保存的機構是 1974年由於國際農業研究諮商組織 (CGIAR) 所籌設之國際植物遺傳資源委員會(IBPGR) ，此委員會的宗旨是『藉著支援並籌設全球性植物遺傳資源的收集及保存工作網，贊助並進行有關之研究以提升世界人類的生活水準』。此委員會訂定了種源探勘、保存、調查、評估與建檔的標準、方法及進行手段。IBPGR 的使命大致如下：

(1) 發展全球性植物遺傳資源中心工作網。

(2) 挽救種源免於喪失或侵蝕，並填補目前收集種源之遺漏，尤其是地方性及野生種。

(3) 建立調查及評估的標準，以使這二項工作更方便，並促進其交流。

(4) 藉由訓練來提升種源庫的理論、技術及管理等各層面人員的素質。
(5) 對不易以一般種子保存的特別作物則發展組織培養技術以收集、保存、並能互相交換。
(6) 對作物的遺傳背景、起源、演化及變異等增加了解。
(7) 建立並實施種子貯存的標準以期能完善的保存種源。

作物的多樣性

同一作物的多樣化是由下列五種因子交互作用的演化結果，即突變、基因轉移、重組、篩選以及遺傳物質流失。前三個因子可以增加變化，而後二個則為固定或消去其變異性。

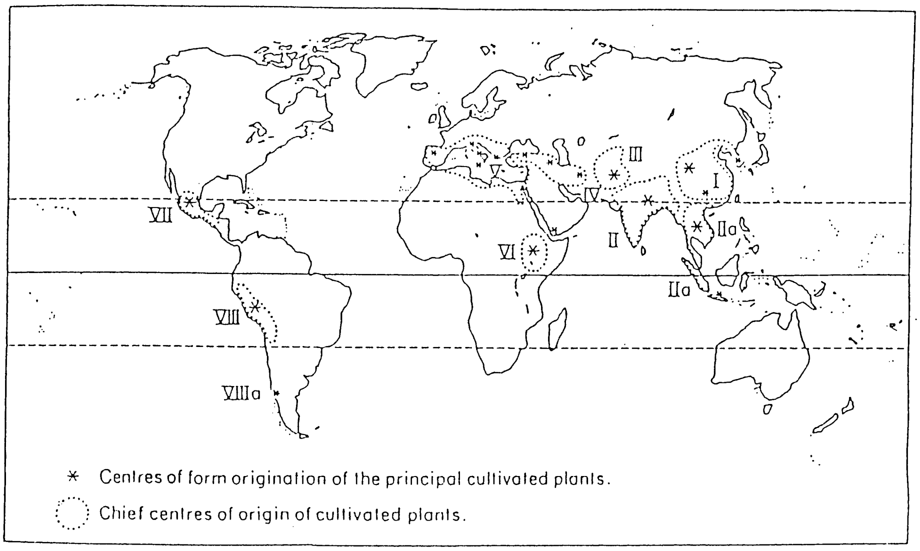
突變在一般情形下發生的機率為 10^{-3}到10^{-6} ；基因的轉移則可以將近緣種或同種不同族群的特點集中造成新雜交種；基因的重組則可使有利生存的組合活下來並固定，而淘汰不良的組合。

植物在被栽培之前及之中的演化情形的知識對能成功保存遺傳資源上是很重要的，因為作物之野生近緣種才能被確認而加以保存，而此工作可避免一般育種者以改良作物眼光所做的淘汰。

馴化的作物中某些特性如不易裂莢的基因，由於其增加了在收獲中所佔之比例而造成了明顯或不明顯的淘選作用。不僅如此，人類也會為了實際或觀賞的緣故挑選出獨特的植株加以繁殖，在此同時自然界的淘選力量則減少了，因為種植可以使一些原本在自然界中無法生存的植株活下來，以上的因子在在都造成了作物的多樣性。尤其是在生態上的差異，如不同樣的果實、莖蔓、根等。更詳細的情況請參加 Simon 的書。

根據　Vavilov 在1926年提出植物多樣化的地理分佈，在全世界共有八個最重要的地區，他稱之為『多樣化中心』(見圖二) 這些中心的相關作物則請參見表一；此八中心均位於南北緯 20° 到 45° 之間，而這些地區同時也是在 7,000到13,000年前開始成為『農業搖籃』。

圖二、 Vavilov 的世界栽培植物發源中心



Vavilov對『發源中心』的概念帶動了後來研究植物分佈的工作，不同的觀點紛紛提出。如今所公認的世界植物種類發源核心以及其外圍之分佈中心則請參見表二。

Vavilov也觀察到這些發源中心顯性基因十分突出，到了中心的外圍隱性基因開始增加了，而變異也逐漸漸少，那是由於自交，基因流失及地理分隔所致，在某些情形下，當環境漸漸不適合原來的主要作物時，隨伴之『野草型』植物或次要作物會變成主要作物，而原來的主要作物則變成野草形式，如大麥、小麥、燕麥等。 同時經由他的研究 Vavilov 也發表了『同化演進』之假說。即在同一地理區內的，不相關作物會有相似之特徵。亦即如果某一特性在某種植物上被發現，似乎可期待同樣的特性也可以在同一區內不相干的另外種類上找到。

表一、Vavilov的八個世界栽培植物發源分佈中心及其相關作物

1. THE CHINESE CENTRE

Avena Nuda, Naked oat (secondary centre of origin)
Glycine max, Soybean
Phaseolus angularis, Adzuki bean
Phaseolus vulgaris, Bean (recessive form : secondary centre)
Phyllostachys spp., Small bamboos
Brassica juncea, Leaf mustard (secondary centre of origin)
Prunus armeniaca, Apricot
Prunus persica, Peach
Citrus sinensis, Orange
Sesamum indicum, Sesame (endemic group of dwarf varieties; secondary centre)
Camellia (Thea) *sinensis*, China tea

2. THE INDIAN CENTRE

Oryza sativa, Rice
Eleusine coracana, Finger millet
Cicer arietinum, Chickpea
Phaseolus aconitifolius, Math bean
Phaseolus calcaratus, Rice bean
Dolichos biflorus, Horse gram
Vigna sinensis, Asparagus bean
Solanum melongena, Eggplant
Raphanus caudatus, Rat's tail radish
Colocasia antiquorum, Taro yam
Cucumis sativus, Cucumber
Gossypium arboreum, Tree cotton, 2x
Corchorus olitorius, Jute
Piper nigrum, Pepper
Indigofera tinctoria, Indigo.

2a. THE INDO-MALAYAN CENTRE

Dioscorea spp., Yam
Citrus maxima, Pomelo
Musa spp., Banana
Cocos nucifera, Coconut

3. THE CENTRAL ASIATIC CENTRE

Triticum aestivum, Bread wheat
Triticum compactum, Club wheat
T. sphaerococcum, Shot wheat
Secale cereale, Rye (secondary centre)
Pisum sativum, Pea
Lens culinaris, Lentil
Cicer arietinum, Chickpea
Sesamum indicum, Sesame (one of the centres of origin)
Linum usitatissimum, Flax (one of the centres of origin)
Carthamus tinctorius, Safflower (one of the centres of origin)
Daucus carota, Carrot (basic centre of Asiatic varieties)
Raphanus sativus, Radish (one of the centres of origin)
Pyrus communis, Pear
Malus pumila, Apple
Juglans regia , Walnut

4. THE NEAR EASTERN CENTRE

Triticum monococcum, Einkorn wheat
Triticum durum, Durum wheat
Triticum turgidum, Poulard wheat

Triticum aestivum, Bread wheat (endemic awnless group; one of the centres of origin)
Hordeum vulgare, Endemic groups of cultivated two-rowed barleys
Secale cereale, Rye
Avena byzantina, Red oat
Cicer arietinum, Chickpea (secondary centre)
Lens culinaris, Lentil (a large endemic group of varieties)
Pisum sativum, Pea (a large endemic group; secondary centre)
Medicago sativa, Blue alfalfa
Sesamum indicum. Sesame (a separate geographic group)
Linum usitatissimum, Flaw (many endemic varieties)
Cucumis melo, Melon
Prunus amvodalus, Almond
Ficus carica, Fig
Punica granatum, Pomegranate
Vitis vinifera, Grape
Prunus armeniaca, Apricot (one of centres of origin)
Pistacia vera, Pistacthio (one of the centres)

5. THE MEDITERRANEAN CENTRE

Triticum durum, Durum wheat
Avena strigosa, Hulled oats
Vivia faba, Broad bean
Brassica oleracea, Cabbage
Olea europea, Olive
Lactuca sativa, Lettuce

6. THE ABYSSINIAN CENTRE

Triticum durum, Durum wheat (an amazing wealth of forms)
Triticum turgidum, Poulard wheat (an exceptional wealth of forms)
Triticum dicoccum, Emmer
Hordeum vulgare, Barley (an exceptional diversity of forms)
Cicer arietinum, Chickpea (a centre)
Lens culinaris, Lentil (a centre)
Eragrostis tef, Teff
Eleusine coracana, Finger millet
Pisum sativum, Pea (one of the centres)
Linum usitatissimum, Flax (a centre)
Sesamum indicum, Sesame (basic centre)
Ricinus communis, Castor bean (a centre)
Coffea arabica, Coffee

7. THE SOUTH MEXICAN AND CENTRAL AMERICAN CENTRE

Zea mays, Corn
Phaseolus vulgaris, Common bean
Capsicum annuum, Pepper
Gossypium hirsutum, Upland cotton
Agave sisalana, Sisal hemp
Cucurbita spp., Squash, Pumpkin, Gourd

8. SOUTH AMERICAN (PERUVIAN-ECUADOREAN-BOLIVIAN) CENTRE

Ipomoea batatas, Sweet potato
Solanum tuberosum, Potato
Phaseolus lunatus, Lima bean
Lycopersicon esculentum, Tomato
Gossypium barbadense, Sea island cotton (4x)
Carica papaya, Papaya
Nicotiana tabacum, Tobacco

8a. THE CHILDE CENTRE

Solanum tuberosum, Potato

8b. BRAZILIAN-PARAGUAYAN CENTRE

Manihot esculenta, Manioc
Arachis hypogaea, Peanut
Theobroma cacao, Cacao (secondary centre)
Hevea brasiliensis, Rubber tree
Ananas comosa, Pineapple
Passiflora edulis, Purple granadilla

表二、 支配性植物的來源核心、分佈地區及外圍中心

Nuclear centres	Regions of diversity	Outlying minor centres
A Northern China	Ⅰ China Ⅱ India Ⅲ Southesat Asia	1 Japan 2 New Guinea 3 Solom Islands. Fiji, and South Pacific
B The Near East	Ⅳ Central Asia Ⅴ The Near East Ⅵ The Mediterranean Ⅶ Ethiopia Ⅷ West Africa	4 Northwestern Europe
C Southern Mexico	Ⅸ Meso-America	5 United States, Canada 6 The Caribbean
D Central to Southern Peru	Ⅹ Northern Andes (Venezuela to Bolivia)	7 Southern Chile 8 Brazil

探勘與收集

種源的收集可以數種方式配合進行：通過交換及贈送或是去探勘並採集；最重要的當屬後者，即原始遺傳物質的收集。

種源收集的目標可以是特定的一個種，特定的性狀，也可以是種群，決定了收集的種後，就要決定採樣方法，而這要依所收集的種而不同，有異於傳統的分類學家的是種源保存者爲能收得此作物的最大遺傳分佈會採集各樣的標本，一個由 Marshall與 Brown 在1975年所設定的採集方式可以收集到 95%以上存在頻率高於 5% 的基因，然而要精確的計算所收集的基因數，在實際上很困難的，除非所收集之族群只有很少的幾株，而能在每一株上採樣。對於一個作物在地理學及物種學上的分佈、整個基因庫的結構與分佈，以及目標區微環境的了解亦十分重要。因爲這可避免在擬定收集計畫時忽略掉一些重要因素，但對於收集目標種的族群、結構經常是不了解的，此時做次行前調查將能免去再一次的重複收集。大多數植物會因常年被地形隔絕，如山谷之間互不相通，而產生相互的差異，而且甚至同一族群內往往有很大的差異存在。農業環境與耕作制度在作物差異的分割上扮演很重要的角色。收集計畫可橫跨許多不同的溫度、降雨量、生長季節、光照度、日長等地區，而這可以收集到同一種植物的許多不同表現形。不同的地形與土壤也會導致植物的差異，所以有等高線而比例爲百萬分之一的地形圖以及道路圖在擬定收集路線時將很有用，而如要更詳細的規劃主要路線旁的支線，則要應用到土壤、氣象、植物相等地圖。

如何選擇探勘及收集的地區呢? 下列數點爲考慮的要項：

(1) 在保存遺傳物質立場上，各作物的優先次序。

(2) 在保存遺傳物質目的下，各地區的優先次序。

(3) 遺傳變異量之預期。

(4) 以前收集、保存的記錄。

(5) 目的區的可接近深入程度。

如果我們期望能收集到更多的變異，即使以前曾經收集過，也可以再做一次的收集，因爲收集或有遺漏，尤其是較難進入行動的地區裡，往往有一些野生種未曾被涵蓋進去。而所收集的種源，也會在保存中發生基因侵蝕，這樣再次的收集就有必要了。

爲了使工作能更有效率 ，一支採集隊大約以 2 到 3 人組成，且至少要包括一位對於該作物及其野生近緣種和農業都十分熟悉的人，另要一位當地人且了解該作物並熟知當地地形、語言與其栽培方式，還要一個司機嚮導。對於該作物在當地的自然環境下的習性，病蟲害的了解，可以對鑑定一些很有用的資料有個準備。收集行動之前也有必要知會當地政府以免不必要的麻煩，而種子的運送清理也要事先安排好，這包括了出口許可、檢疫以及其他紙上作業，在某些國家的某些地區在進入以前還得申請警方的許可，運送和預定的種源庫也得聯絡好，往往不能適當的送達種源庫而使一些辛苦收集的樣品喪失掉，而所有收集的樣品也得在所在國國家內有另一份的保存。收集之後就保存、評估及利用的關係上要和來源國家保存聯繫。這樣才能有足夠的資料認識那需要進一步收集的地區並得到更多的合作。

要選擇適當的時機進行採集工作，並且考慮以下事項：在可以收集的時間內收集到最多的變異，在植物成熟時期進行採集，同一地區可在許多不同的地點收集，就當地不同的土壤、氣候、海拔、耕作制度等進行不同的收集。在田地的周圍收集一些野生植株並收集野生近緣種，但是由於季節的不同，通常在一年內可進行二個不同季節的收集。

採集行動要有下列裝備：

(1) 收集裝備：採樣、記錄、裝運等工具。

(2) 科學儀器：測方向、海拔、酸鹼及處理樣品之工具。

(3) 交通工具：適合地形之機動車輛、維修工具‧‧‧‧等。

(4) 露營設備：炊具、寢具等。

(5) 適合當地的衣物。

(6) 各類藥品：驅虫、胃腸、蛇毒等。

以上裝備之詳細內容與其用途均能在 Hawkes 的書中找到詳盡的描述。

收 集 地 區

收集工作通常在下面四種地方進行(1)農民田裡(2)家庭果、菜園(3)農家貯藏室(4)野外生長地；大多數的情況下是以農田爲主要目標，因爲在田裡可以立即觀察到生態、生理性狀、並依其變異性採樣，不僅如此，農田也許是唯一能順利執行採樣計畫又能記錄田地與植物狀況的地方。

採集的方針是根據植物的種、族群間基因的異同，以及採集地的地理狀況而定，如果不能得到足夠的參考資料，通常可採用『粗略網狀採樣法』(即全區以逢機方式，固定間隔採樣)，而採樣的頻度則依照目標區之環境的變化而定。當氣候、土壤形態、植物相、耕作地、作物及海拔都很一致時，可以設定每隔20～25公里爲一採集點，而如果以上因子的變化很大的話，尤其是海拔

的變化，那採集點的間隔可以小於一公里，甚至每100公尺海拔的變化就要做一次採樣。

在粗略網狀採集後，可以計畫進一步較詳細的採集，尤其是發現有較大變異的地方可以做再次的採集，而這二個階段的採集最好分在二個季節進行，這樣可以採集到生長在不同季節的族群樣品，而在每一採集點要以逢機的方式採取繁殖體如果實、根莖等。採集點的大小可由 5X5公尺到 50X50 公尺，這得取決於族群的大小及植株的密度， 一般言每個採集點所採的樣品編成一號，但是若有任何可以明顯區別的特殊個體，得分開另行採集。採到樣品之後，有關種子的萃取及清潔工作，可以於夜間在帳篷內或旅館中進行。

在探勘、採集中，收集工作的乏味以及在同一採集區沒能有足夠時間停留往往是田間採集工作上的問題；因此由農家的貯藏室、小店、或當地市場收集也是十分重要的，而且該個種源的一些必要資料如名稱、用途、種植季等也能從擁有者更多、更詳盡的得到；在農家貯藏室中收集的另一個好處就是能把該農民所有的品種一次收集完成；收集中必然會有品種混雜的情況，但仍得收集，純化工作可以在種源庫另外進行。

就園藝作物而言，在家庭的果、菜園中收集，可能較之在他處收集更能得到較多的變異，說不定會上百，而且『遺傳侵蝕』較少。在某些國家中，以上的地點也許是唯一值得去收集的，因爲大多數經濟作物在較大規模的栽培中，均只有很齊一而極少變異的改良品種。

採集根或莖的工作更是困難，因爲得花時間去挖掘地下部，成熟的時間也很短暫、運輸上也有問題，更難保持其活力，而營養繁殖習性之相異也使採樣發生問題。如果找不到成熟的地下部的話，得剪取地上的莖葉等，而問題在於如何使剪下的部分活下去。目前正嘗試以組織培養技術來解決問題。

在收集的時候，種源本身以及田野的情況資料都要記在收集表上，這些資料將會轉到負責貯存種源的種源庫之資料庫中，收集表有多種，圖三是亞蔬中心的形式。時間如果許可的話，植物標本可以收集以做爲分類之參考，而採集隊日誌也應該詳細的填寫，以備在將來必須時可以做爲參考的資料，而對於重要的植株或採集地點也可以用照片或幻燈片拍照下來做爲記錄。

種源的保存

在植物遺傳資源工作上，保存是一項很花錢的事，採用的方法則取決於要保存的種及其族群狀態，以及保存的目的何在，大略而言，保存方法可分爲自然狀態下(in situ) 及非自然狀態下(ex situ)二種。

自然狀態保存，如同字面上所指，就是將要保存的一個種，找一個原產地保持其自然生長情況。此方法適用於一些目前比較沒有農業上重要性的植物，也就是一些半馴化或根本是野生的族群，如一些原始的蔬菜、果樹、林木以及牧草等，這些植物不必依靠人類來繁殖。通常一些自然保護區如國家公園、森林保護區等，都能容許多種植物的生態系統存留，但此方法至今尚未健全，只是很清楚能知道的是，如果要有更好的成效，必須在技術上、經濟上、及政治上同時努力。而我們知道生態地理系統的調查必須由優先順序、基因庫、地區、種等來做決定，而那是既費時又昂貴的。一個生物保護區的概念是：一個受嚴密保護的核心區外圍環以一道緩衝區，在緩衝區內可以大力提倡進行研究、旅遊、教學等活動，而此緩衝區外再繞以人類之墾殖地做爲次一級的緩衝，因此保護區是否能成功，取決於當地人民的作爲。要注意的是此方法不適用於已馴化之作

圖三、亞蔬中心種原收集記錄表

AVRDC-BRBU COLLECTION RECORD SHEET

COLLECTING INSTITUTE ____________
COLLECTORS ____________
COLLECTION NO. ____________
DATE OF COLLECTION ____YR/____MO/____DD
COUNTRY ____________
DISTRICT/PROVINCE ____________
LOCATION OF COLLECTION SITE
name of village: ____________
nearest town: ____________
distance (in km) : ____________
direction: ____________
GROWER NAME ____________

LATITUDE OF SITE ____________
LONGITUDE OF SITE ____________
ALTITUDE OF SITE ____________ (m)
SITE TEMPERATURE: Max____Min____Avg____
SITE RAINFALL: Max____Min____Avg____
CROP COLLECTED ____________
GENUS ____________ SPECIES ____________
VARIETY/LOCAL NAME ____________
MEANING ____________
VARIETY NAME LANGUAGE ____________
USAGE (specify) ____________
____

COLLECTION SOURCE:
1. farmland
2. backyard/home garden
3. farm store/threshing place
4. village market
5. commercial seed shop (name ____)
6. agricultural institute
7. bordering field
8. natural vegetation/wild
9. others (specify) ____________

GENETIC STATUS:
1. wild
2. weedy
3. primitive cultivar/landrace
4. improved OP cultivar
5. hybrid cultivar
6. others (specify) ____________

SAMPLE TYPE:
1. single plant
2. pure line/clone
3. mixture/population (clone/pureline)
4. open-pollinated
5. others (specify) ____________

SAMPLING METHOD:
1. random
2. non-random (specify) ____________

MATERIAL: 1 seed; 2 fruit; 3 pod;
4 others (specify) ____________

CULTURAL PRACTICE:
shifting: Yes; No
terraced: Yes; No
direct seeding: Yes; No
transplanting: Yes; No
intercropping: Yes; No
intensive: Yes; No
rotation crop: Yes; No
irrigated: none; by hand; furrow; overhead; drip

HERBARIUM SPECIMEN: Yes; No
PHOTOGRAPH: Yes; No

SOWING MONTH: ____________
TRANSPLANT MONTH: ____________
HARVEST MONTH: ____________

TOPOGRAPHY:
1. swamp 2. flood plain
3. level plain 4. undulating
5. hilly 6. mountainous
7. others (specify) ____________

SITE:
1. level 2. slope
3. plateau 4. depression

SOIL TEXTURE:
1. sand 2. sandy loam
3. loam 4. clay loam
5. silt 6. clay
7. highly organic (peat/muck)
8. others (specify) ____________

DRAINAGE:
1. poor 2. moderate
3. good 4. excessive

SOIL COLOUR:
1. black 2. dark brown
3. light brown 4. grey
5. yellow 6. red
7. others (specify) ____________

STONINESS:
1. none 2. low
3. medium 4. rocky

DISEASES AND PESTS: ____________
____
____
____

NOTES: (Associated wild, weedy and crop species, special plant characters and morphological variation, status of genetic erosion, other observations).
____
____
____
____

物，因為要規定農民不得以更有經濟價值的改良種去取代當地土種是不行的。

非自然狀態保存就是把植物保存在非其自然生育的狀態下，其與自然狀態保存的最基本不同處在於自然狀態保存容許族群在被保存中繼續演化，而非自然狀態保存則在找尋保存的種源族群中有無遺漏的基因，非自然狀態保存的植物可能是種子、全株植物、植物的一部分，種源庫中的組織培養或細胞培養、田間種源，而目前-196℃的液態氮超低溫保存技術正在嘗試發展中。

種子是最方便保存的植物體，其不僅體積小而且在乾燥、清潔、包裝上都很容易處理，然而這只是指一般『正統』的種子才能，也就是這類種子是能被乾燥到相當低的含水量，而且能在低溫環境下生存，而另外一種『非尋常』的種子就無法忍受含水量的降低。目前一般所謂的種源庫，大多數為貯藏庫形式，貯藏庫有長、中、短期三種，長期貯存是在收集保存『正統』的種子的基本貯藏。所謂基本貯藏是不用於分贈種子的，而是用來應付萬一流失品種的。國際植物遺傳資源委員會推荐的長期貯存條件是種子含水量為 5±1% (除了一些高含油種子為 7-8%)，貯存溫度則為 -18℃。種子要在除濕機控制下緩慢的乾燥(15℃及15% RH)，並且用鋁箔袋完全密封包裝起來，種子的活力則須定期檢查，並且在發芽率低於 85%時重新繁殖，在此條件下，有些種類可以保存一百年以上，國際植物遺傳資源委員會也推荐了保存量，為 3,000～4,000 粒種子。

中期保存在運作上通常為應用貯存，其貯藏條件不若長期者嚴苛，因此保存期限也就較短，種子可以由應用貯存提出來分贈需要的人，或拿來做調查、評估等工作，種子存放在不完全密封而可隨意開啓的容器中，保存於 2±3℃及40±5% RH (亦即可以保持種子含水量在6～8%)的環境中，這種作法是為能便利的拿取種子。

短期貯存只是為仍在處理中的種子做為臨時存放的地方，其溫濕度控制在15℃及40% RH左右，目地在減少昆虫的活動到最低。

非自然狀態保存的另一種形式為田間種源庫，這是將植物栽培於田裡的保存方式，這種方式適於保存生產『非尋常』種子的作物，以營養體繁殖的作物，性功能貧乏的作物，異質結合之樹木等等。植物園在這種田間種源上擔當了重要的功能，這提供了可以立即作研究利用的植物材料；但這需要相當大面積的土地，因此其花費比起以種子方式的保存又多了許多，而且這方式也更容易遭受包括生物或非生物性的災害。

人工環境保存(in vitro)是將植物保存在組織培養中，通常是採用取生長點繁殖的方式，因為這比較穩定，也就是說比較少突變，組織培養通常是用來補償田間種源無法做到的事；在緩慢生長控制下，集合了大量的栽培種於一處，尤其能消除病毒，而且組織培養中的無病毒苗較能通過國際間的植物檢疫合格標準。此一保存方式的主要顧慮為在長期『緩慢生長』狀態下植物遺傳物質的穩定性。目前有關這方面的知識仍很缺乏，尙待進一步的研究。

植物遺傳資源保存的最終解決方式可能會是利用超低溫冷凍保存，亦即將種子或組織培養中植物冷凍在極低的溫度下， 例如液態氮的 -196℃，在如此的低溫下，一切生物機能實際上已停止，而種源或許就因此被保存下來，運用此技術的主要問題在於冷凍前的處理以及解凍的程序，但至今尙無安全且可以遵循的規則或方法，可以用在植物組織上。

國際植物遺傳資源委員會在許多國家中，地區間以及國際上建立了種源庫的『全球工作網』，主要的工作在於分配每個種源庫做特定作物的基本貯藏，而且另外放一套在另一個地方以保安全，『全球工作網』的情況列於表三。

表三、種子作物全球基本貯藏工作網(IBPGR 1988)

Crop	Species covered	Scope of collection						Institute、
		Glo-bal	Eur-opean	Afri-can	Asi-an	Regi-onal	New World	
Cereals	Barley	v						PGR,Ottawa,Canada
			v					NGB,und,Sweden
				v				PGRC/E,Addis Ababa,Ethiopia
					v			NIAR,Tsukuba,Japan
						v		ICARDA
	Maize						v	NGPS,USA
					v			NIAR,Tsukuba,Japan
					v			TISTR,Bangkok,Thailand
			v					VIR,Leningrad,USSR
						Mediterranean		Portuguese Genebank, Braga Portugal
Millets	*Pennisetum*	v						NPGS,USA
	Pennisetum	v						PGR,Ottawa,Canada
	Pennisetum	v						ICRISAT
	Eleusine	v						PGRC/E,Addis Ababa,Ethiopia
	Eleusine	v						ICRISAT
	Minor Indian millets					v		NBPGR,New Delhi,India
	Eragrostis	v						PGRC/E,Addis Ababa,Ethiopia
	Panicum miliaceum	v						ICRISAT
	Setaria italica	v						ICRISAT
Oats		v						PGR,Ottawa,Canada
		v						NGB,Lund,Sweden
Rice	*Oryza sativa-*							
	indica	v						IRRI
	javanica	v						IRRI
	japonica	v						NIAR,Tsukuba,Japan
				v				IITA,Ibaden,Nigeria
						v		NPGS,USA
	Wild species	v						IRRI
Rye		v						Polish Geneban, Radzikow
		v						NGB,Lund,Sweden
Sorghum		v						NPGS,USA
		v						ICRISAT
Wheat	Cultivated spp.	v						VIR, Leningrad, USSR
		v						CNR,Bari,Italy
		v						NPGS,USA
						v		CAAS, Beijing
	Wild species (*Triticum and Asgilops*)							Plant Germplasm Institute,University of Kyoto,Japan
Food Legumes	Chickpea	v						ICRISAT
		v						ICARDA
	Faba bean	v						CNR,Bari,Italy
	Groundnut	v						ICRISAT
						South American		INTA,Pergamino,Argentina
	Lentil	v						ICARDA

Crop	Species covered	Scope of collection: Global	European	African	Asian	Regional	New World	Institute
	Lupin	v						ZIGuk, Gatersleben, GDR
			v					INIA,Madrid,Spain
	Pea	v						NGB,Lund,Sweden
						Mediterranean		CNR, Bari, Italy
						Central and East European		Polish Genebank, Radzikow, Poland
	Phaseolus Wild spp.	v						Faculte des Sciences Agron.de l'Etat, Gembloux,Belgium
	Cultivated spp.	v						CIAT
	Cultivated spp.	v						NPGS,USA
			v					FAL,Braunschweig, FRG
	Pigeonpea	v						ICRISAT
	Soyabean	v						NIAR, Tsukuba, Japan
		v						NPGS,USA
	Wild perennial	v						CSIRO, Canberra, Australia
	Vigna Wild spp.	v						Facúlte des Sciences Agron.de l'Etat, Gembloux,Gelgium
	V. radiata	v						IPB,Los Banos,Philippines
		v						AVRDC, Taiwan, China
	V. unguiculata	v						IITA
		v						NPGS, USA
	Winged bean	v						IPB, Los Banos, Philippines
		v						TISTR,Bangkok,Thailand
Root Crops	Cassava(seed)	v						CIAT
	Potato(seed)	v						CIP
	Sweet potato(seed)	v						NPGS, USA
					v			AVRDC, Taiwan, China
		v						NIAR, Tsukuba, Japan
Vegetables	*Alliua*	v						CGN,Wageningen,Netherlands
		v						Institue of Horticulture,Wellesbourne,UK
		v						NPGS,USA
						South and East European		RCA,Tapioszele,Hungary
					v			NIAR,Tsukuba,Japan
	Amaranthus	v						NPGS,USA
					v			NBPBR, New Delhi, India
	Capsicum	v						CATIE,Turrialba,Costa Rica
		v						CGN, Wageningen, Netherlands
	Cruciferae Brassica							
	carinata	v						FAL,Braunschweig,FRG
	B.carinata	v						PGRC/E, Addis Ababa, Ethiopia
	B.oleracea	v						CAAS, Beijing, China
	B.oleracea	v						Institute of Horticulture,Wellesbourne,UK
	B.oleracea	v						CGN,Wageningen,Netherlands
	Raphanus	v						CAAS, Beijing, China
	Raphanus	v						Institute of Horticulture,Wellesbourne,UK
	Wild spp.	v						Universidad Politecnica,Madrid,Spain
		v						Tohoku University,Sendai,Japan

Crop	Species covered	Scope of collection: Global	European	African	Asian	Regional	New World	Institute
		Glo-bal	Eur-opean	Afri-can	Asi-an	Regi-onal	New World	
	Oilseeds and green manures: *B.campestris*, *B.juncea*							PGR,Ottawan,Canada
	B.napus, *Sinapis alba*	v						FAL, Braunschweig, FRG
	Vegetables and fodders: *B.campestris*, *B.juncea*,*B. napus*	v						Institute of Horticulture,Wellesbourne,UK
	B.napus	v						FAL,Braunschweig,FRG
	All Cruciferae crops					East Asian		NIAR, Tsukuba, Japan
Okra		v						NPGG, USA
Tomato		v						CATIE, Turrialba, Costa Rica
		v						ZIGuk, Gatersleben, GDR
		v						NPGS, USA
					v			IPB, Los Banos, Philippines
Southeast Asian vegetables						v		IPB, Los Banos, Philippines
Cucurbit-aceae	*Benincasa*,Luffa *Monordica*, *Trichosanthes*	v						IPB, Los Banos, Philippines
	Cucumis,*Citrullus*, *Cucurbita*	v						NPGS, USA
	Cucumis, *Citrullus*	v						INIA, Madrid, Spain
Eggplant		v						CGN,Wageningen,Netherlands
		v						NPGS, USA
Indus-trial Crops	Beet	v						FAL, Braunschweig, FRG
		v						NGB, Lund, Sweden
						Mediterranean		Greek Gene Bank,Thessaloniki
	Cotton					Mediterranean		Greek Gene Bank,Thessaloniki
	Sugarcane(seed)	v						NIAR,Tsukuba,Japan
		v						NPGS,USA
	Tobacco					Mediterranean		Greek Bene Bank,Thessaloniki
Forages Legumes	*Centrosema*	v						CIAT
		v						CENARGEN, Brazil
	Desmodium	v				CIAT		
		v						CSIRO,Brisbane,Australia
	Desmanthus	v						CSIRO, Brisbane, Australia
	Stylosanthes	v						CIAT
		v						CSIRO, Brisbane, Australia
	Leucaena	v						NPGS, USA
	Lotononis	v						ILCA
		v						Seed Bank, RBG, Kew UK
	Macroptilium	v						CENARGEN, Brazil
		v						CSIRO, Brisbane, Australia
	Neonotonia			v				ILCA
								Seed Bank, RBG, Kew, UK

Crop	Species covered	Global	European	African	Asian	Regional	New World	Institute
	Zornia	v						NPGS, USA
								CIAT, Colombia
	Trifolium			v				ILCA
		v						Seed Bank, RBG, Kew, UK
	Grasses *Cynodon*	v						NPGS, USA
	Cenchrus	v						Seed Bank, RBG, Kew, UK
								ILCA
								CSIRO, Brisbane, Australia
	Dioitaria	v						ILCA
								CSIRO, Brisbane, Australia
								Seed Bank, RBG, Kew UK
	Pennisetum	v						NPGS, USA
	Paspoalum	v						NPGS, USA
	Urochloa	v						CSIRO, Brisbane, Australia
Others	Tree spp.						(Fuel and environmental stabilization in arid areas)	Seed Bank, RBG, Kew, UK

由於田間收集來的種子品質及數量通常不足，所以繁殖往往是種源保存的第一步工作，而當長期貯藏的種子活力或中期貯存的種子數量降到設定之標準時，也要進行繁殖工作，而更新的工作主要目的在保持原來的一切遺傳物質，Frankel在1981年曾建議至少種植100株逢機選出的植株。

調查與評估

調查是記錄植物的可遺傳，在不同環境下都很穩定，且很容易以肉眼觀察區別的特性，這通常是指生態特性，因此調查工作並不困難，但卻得對所收集的每個品種都做；由於這是一樁既乏味又耗時、費錢的例行工作，因此也是種源保存工作中最容易被忽視的，但所收集品種的利用也因此受到阻礙。

調查能提供許多有用的資料，確定我們所收集東西的特點，在一大堆不同的性狀中可以用來做分類依據，以劃分出小群，確認重複的品種，找出收集各種變異的遺漏處，以便做進一步收集時的參考等。一個沒有詳盡調查資料的種源庫只能像個博物館似的，能保存品種，但無法充分利用。

評估工作是更進一層的篩選工作，經由受專業訓練的人員及科學家去確認其中對於生物或非生物性生存壓力的抗力，包括了虫害、病害、鳥害、不同的土壤反應，惡劣的環境如淹水、乾旱、鹽分等，而食物營養價值也是評估對象之一。可以說評估工作是針對一些特別的性狀，要一項

項的由各別的專業人員來執行，且通常得在一般性篩選工作之前完成，也就是說這又是個省時省錢的工作。

由國際植物遺傳資源委員會所出版的作物描述手冊，提供了很好的描述與標準，每個作物的描述手冊均由三部分組成：來源資料、調查資料及評估資料。來源資料中較重要的如品種名稱、辨認號碼、來源或產地特點等，而調查與評估已如上所述。到目前爲止，國際植物遺傳資源委員會已出版的作物描述手冊共有四十種。(見表四)

表四、國際植物遺傳資源委員會已出版的作物描述手冊一覽 (到1988年)

Almond Descriptors (Revised)
Apple Descriptors
Apricot Descriptors
Bambara Groundnut Descriptors
Brassica campestris L. Descriptors
Cashew Descriptors
Cherry Descriptors
Chickpea Descriptors
Citrus Descriptors
Cotton Descriptors
Cowpea Descriptors
Echinochloa Millet Descriptors
Eggplant Descriptors
Faba Bean Descriptors
Finger Millet Descriptors
Forage Grass Descriptors
Forage Legumes Descriptors
Grape Descriptors
Groundnut Descriptors (Revised)
Kodo Millet Descriptors
Lentil Descriptors
Maize Descriptors
Mango Descriptors
Oat Descriptors
Panicum millaceum and *P. sumatrense* Descriptors
Phaseolus acutifolius Descriptors
Papaya Descriptors
Peach Descriptors
Pearl Millet Descriptors
Plum Descriptors
Potato Variety Descriptors
Rice (Descriptors for Rice *Oryze satova* L.)
Rye and Triticale Descriptors
Setaria italica and *S. pumila* Descriptors
Sorghum Descriptors (Revised)
Soyabean Descriptors
Sunflower Descriptors
Viona aconitifolia and *V. trilobata* Descriptors
Vigna mungo and *V. radiata*, Descriptors for (Revised)
Wheat, Descriptors for (Revised)

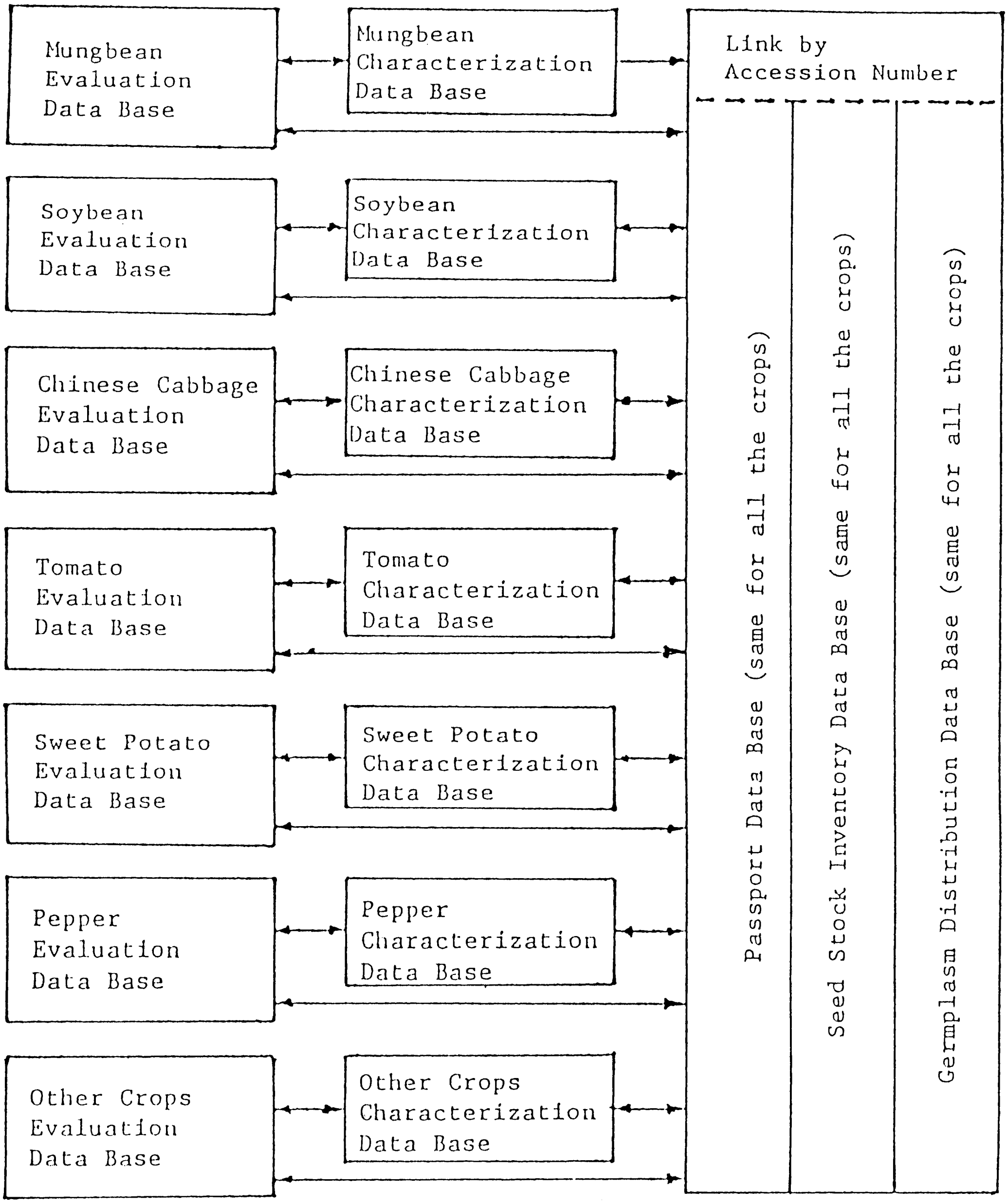
建　　檔

種源庫的收藏到分贈是一套很複雜的程序，有一些相當大數目的資料要保存起來做爲參考，一個種源庫的運作是很昂貴的，而其投資也是長期性的，因此一套高效能電腦化資料管理系統，在種子處理及尋找品種上可以節省許多人力，而這套系統必須涵蓋樣品的資料如來源、調查與評估等，以及種子處理的資料如存放及分送等資料，種子處理資料可以提供種源庫管理上一個能隨時核對種子庫存量、種子活力、需繁殖品種以及種子分送等資料，一個有效率的管理系統可容許工作人員有更多的時間來維持種源的完整，也能有更多的時間投注在調查及評估上。

一個資訊系統的有沒有用，端在其對於複雜要求下找尋資料的效率，這套系統應能接受所有與種源有關的資料，目前有各種不同的電腦軟體及硬體已很成功的在管理種源庫的資料，以亞蔬

中心爲例，MINISIS 軟體用在HP3000迷你電腦上是目前使用的系統，而資料的基礎，架構設計是在於能在MINISIS 的工作條件下，同時管理許多不同種作物的資料。來源、庫存及送出的資料在各作物上都是一樣，因此我們將這些放在同一個資料庫中，然而調查與評估卻是有其獨特性（每一作物各有其不同的描述項目）。所以這方面的資料，就是各個作物自成一資料庫，圖四顯示了亞蔬中心種源庫的各電腦資料庫的相互關係，在亞蔬中心共有16部終端機可同時在資料庫中尋找所需資訊。

圖四、亞蔬中心種源庫，電腦化資料系統架構(所有的相互連接均以作物在亞蔬中心的登錄號碼 accession number 爲依據)



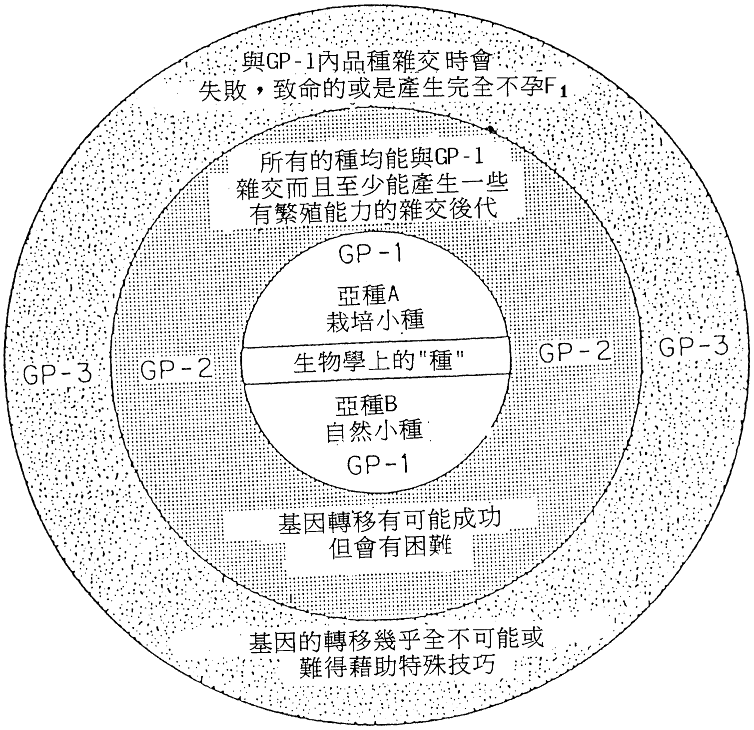
輸入資料的準備工作也是十分要緊的；國際植物遺傳資源委員會已經對於作物的各項資料有個標準化的制度，一些易懂、易用的資料表格，對於輸入及核對資料將可大大的節省人力。

種源的利用

種源保存的最終目的就是能用來改良作物，如以上所述，各種的評估能增進使用種源的效率，對一個作物之基因庫的分級及演化研究可以幫助我們了解作物不同的族群、生態形、亞種、栽培種群以及種在基因庫中的相互關係，進而能了解其血緣與雜交能力。

Harlan 與 de Wet 將作物的基因庫概分爲三級，原級 (GP-1)、第二級(GP-2)、以及第三級 (GP-3) 基因庫，由於使用的觀點不同，所以這種分級與分類學可能不盡相符。 有些野生種可能部分在GP-1，部分在GP-2另有在 GP-3的，但 GP-1包含了作物所有的地方性品種，如玉米的GP-1中包含了*Zea may*的品種及其野生近緣種 *Z. mexicana* 以及 *Z. diploperemis*；GP-2則包含了野生的 *Z. perennis*與 *Z. Tripsacum*；而 GP-3 則包含了其他更多的野生種。

圖五、 Harlan 與 de Wet 所提出的作物基因庫分級示意圖



原始基因庫涵蓋了作物中很容易彼此雜交，並產生後代的遺傳物質，亦即基因的轉移毫無問題，一般的育種也是在此階段進行，把一些基因設法轉移到我們要的品種內，可是當我們所要的基因在GP-1中找不到時就得考慮使用GP-2，而GP-1與GP-2之間的雜交是可能的，但常常產生不孕的後代，但也許會有具繁殖能力的後代產生，亦即是基因的轉移雖有困難仍屬可能，而GP-3也可能和GP-1雜交，但其後代全然不孕，因此基因的轉移就需要用上特殊技巧了，只有在GP-1與GP-2

都找不到所要基因時才會使用 GP-3。

在實際的育種工作上，育種家們都比較興趣於遺傳性質的立刻改善，並能馬上發表新品種。因此大家也都喜歡使用血緣較近的品種以達此目的。不過萬一野生種必須被使用時，或者得使用種間雜交來得到所要的基因，那麼對於目標種之間血緣關係的了解(基於基因庫分級)可以使雜交計畫找到最佳的途徑。有鑒於此，演化及雜交前的研究，將會成爲種源研究中心的一大課題。

未來之展望

過去二十年來，植物遺傳資源保存工作的進展與完全，已造成了世界性的對於保存人類共有財產之覺醒。國際植物遺傳資源委員會在收集、保存、調查、評估、資料管理、人員訓練及種源利用上所做的工作，促進了已開發及開發中國家在種源上的工作。但是以我們的經驗，尤其是在開發中國家可以看到這是一樁花費龐大卻又不能立即見到收獲的工作,爲了讓保存種源工作持續前進、必須繼續投入資金。而機構之間的合作關係在『全球種源庫工作網』的推動下，可謂成功。

生物科技的進展將來可能對種源保存工作有革命性的影響，如組織培養與細胞培養技術已增進了大批無病毒種源的繁殖與交流，而花粉、花藥等培養則成了育種利器，對於遠緣的雜交胚培養與雄不稔使之成爲可能，其他尙有微注射在引入染色體及核基因上有了突破。最令人振奮的是分子遺傳學上的基因轉移技術，可以把一特定基因引入另一個體中並使之充分表現，在毫無關係的種間也能進行轉移，如此未來可能整個遺傳物質的保存內容會完全改變。

同時 RFLP 技術在辨認重複品種及建立親緣演化工作上也有相當的助益，此方法的重點在於比較 DNA 本身，而不是比較其衍生物。 而超低溫冷凍保存種子與人工培養組織也正在繼續發展，而這也許能立即解決產生『非尋常』種子植物的遺傳資源保存工作的問題。

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植物種苗法介紹

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種苗為作物生產之根源，為促進品種改良，確保種苗品質，保障農民和育種家之權益，歐、美、日等科技先進國家多訂定實施種苗法，以維護農業之正常合理發展。以往，我國種苗之繁殖推廣與銷售尚乏完整之管理制度，關於新品種之命名雖有『臺灣省農業用動植物及微生物新品種登記命名辦法』之省單行法規，惟內容簡略，又無權利登記之規定，對育種者欠缺保障，對不良種苗商，亦因無法律依據，難以取締。至植物種苗之管理，則係依據『臺灣地區種苗業管理規則』及『臺灣地區學術性農林作物種子與種苗輸出管理辦法』辦理，惟該兩種法規，所規範之範圍有限，已難因應目前之實際需要，且新品種權利之賦與及撤銷，禁止推廣、銷售未經命名登記之品種，檢查種苗業者之設備，及業者違反規定之處罰等事項，均涉及人民權利義務事項，尤須以法律定之。因此，行政院農業委員會參酌歐、美、日等國植物種苗之立法例，並參照我國國情與農業經營之特性，研擬『植物種苗法草案』，於七十七年十二月五日完成立法程序，公告施行。

『植物種苗法』規範內容主要包括以下二部分：

(一)新品種命名及權利登記：主要包括新品種的定義、登記作物種類範圍及權利年限、新品種登記之申請、審查、核准、撤銷及異議程序，核准登記新品種之權利及義務、違反規定之罰則等；其目的在使育種家研究育成或發現的新品種受到合理的保障，鼓勵優良作物品種公諸於世，以加速作物品種改良步伐，提昇農業生產效率及品質；亦是維護農業智慧財產權的具體表現。

(二)種苗管理：主要包括種苗業者的登記及管理、種苗品質、包裝、標示之規範及檢查種苗輸出入管理及違反規定之罰則等。其目的在於保障種苗消費者，使其取得之種苗，為高品質之優良品種，避免不良種苗無限制流通，以建立健全之種苗產銷制度。

至於植物種苗法各項條文內容重點，簡述如下：

(一)立法宗旨及適用法律順序：本法制定目的在實施植物種苗管理，保護農民及新品種之權利，促進品種改良，以利農業生產。本法未規定者，適用其他法律之規定。(第一條)

(二)本法之各級主管機關：參照一般立法例，明定本法所稱主管機關，在中央為行政院農業委員會，在省（市）為省（市）政府，在縣（市）為縣（市）政府，以明權責。(第二條)

(三)新品種之定義及適用範圍：新品種係指具有與現有品種能辨別之一個以上顯著重要特性，且主要性狀具有相當遺傳性與穩定性之植物群體，惟植物種類繁多，為使本法之適用漸進可行，適用本法之植物種類，授權由中央主管機關指定公告之。(第三、第四條)

(四)新品種登記之種類及效力：育種者或發現者所育成或發現之新品種，具有利用價值者，得依本法申請命名及權利登記。命名登記係賦與新品種一特定名稱，以使公衆週知，並與其他品種相

區別，經命名後任何人均可推廣及銷售該品種；至於權利登記則係賦與權利人專有推廣、銷售及使用新品種之權，他人除供作育種材料或小型研究試驗外，非經權利人同意，不得推廣、銷售或使用。對於新品種之研究，有不欲享有專用權，而願大量推廣者，如公立研究機構之成果，僅可申請命名登記。但欲辦理權利登記者，應與命名登記同時申請，因命名登記以後，任何人均可推廣、銷售或使用，爲免發生困擾，宜明定不得於事後補辦。（第五條、第七條、第八條）

五、不予權利登記之新品種項目：命名登記前已推廣銷售之新品種，顯已喪失新穎之特性；又一般糧食作物之新品種，屬重要民生物資，爲免因受新品種權利保護而妨礙作物之生產，爰規定均不予權利登記。(第六條)

六、申請登記之程序：育種者或發現者申請新品種命名及權利登記，應檢具申請書詳述種類、名稱、來源、特性、育成經過、栽培試驗及其他規定事項，必要時並提供材料供性狀檢定，且登記之申請權得讓與或繼承；而二人以上申請登記之品種或名稱相同時，以最先備齊証件提出者爲優先，以確立申請先後之順序。(第九條、第十條、第十一條)

七、新品種登記之審查程序：新品種申請登記之審查，由中央主管機關（農委會）設立新品種審議委員會負責辦理；經審查後，應將審查結果於審定書中敘明，並通知原申請人；其合於命名或權利登記之新品種，審定結果及品種特性由中央主管機關公告週知。公告三個月，期滿無人提起異議者，即爲審查確定，發給新品種命名或權利登記證書。（第十二條、第十四條、第十五條、第十八條)

八、新品種登記之救濟程序：新品種登記經審定公告後，任何人認爲有違反第五條、第六條第一項規定，或利害關係人認有不合第十條規定者，得提起異議；對於不予新品種登記之審定，或對審定公告之新品種經提起異議對異議審定不服者，關於非技術事項，循訴願及行政訴訟程序救濟；對於第九條第一項第三款至九款所定事項不服者，係屬技術性之專門技術範疇，則以再審查，複核方式爲之，俾由中央主管機關所設由具有專門學術或技術人員組成之再審查委員會予以再審查及複核，以資救濟。(第十五條、第十六條、第十七條)

九、新品種權利之期限：歐美採取植物新品種保護立法之國家，對新品種權利保護期間有規定十八年至二十五年者不等，衡酌我國氣候及品種特性，權利保護年限定爲十五年，自審定公告之日起算，至期滿日消滅。惟於品種權利期間內，如權利人死亡而無繼承人者，權利人自行放棄者，或權利人未依規定繳納年費者，其權利亦當然消滅。(第十九條、第二十七條)

十、新品種權利之歸屬：新品種權利屬於無體財產權，可以讓與或繼承；其權歸屬變更時，須以書面向中央主管機關申請變更登記；爲減少共有之權利，因轉移或使用上發生糾紛，規定權利共有人如欲轉讓其應有部分，須先取得持分三分之二以上共有人同意。至於雇用人及受雇人對於育成新品種權利之歸屬；明定除契約另有約定外，受雇人育成之新品種權利屬雇用人所有；但雇用人必須給與受雇人相當獎勵金，以保障受雇人之權利。

(第二十條、第二十一條、第二十二條、第二十三條)

十一、督促新品種之儘速推廣：經核准登記之新品種應於一定期間內從事推廣、銷售、違反者中央主管機關得撤銷其權利登記，以防止新品種權利人爲圖謀暴利故意不從事繁殖推廣或僅作小量繁殖銷售，有違本法促進品種改良，增進農業生產之目的。(第二十八條)

㈢種苗業者之管理：經營種苗業者，應先經主管機關核准並辦理登記，登記後滿六個月尚未開始營業或開始營業後自行停止營業並滿一年而無正當理由者，得撤銷其登記；銷售之種苗，應依中央主管機關所定之標示事項予以標明；主管機關並得派員檢查業者之設備、應具備條件、銷售種苗之品質及是否按規定標示營業，其有違反規定者，並通知限期改善、防治或禁止銷售，以健全管理制度。（第三十一條、第三十三條、第三十四條、第三十六條）。

㈣自國外引進新品種及種苗輸出入之限制：凡由國外引進之新品種，應經農業研究或試驗改良機構作適應性及區域性試驗，經核准命名登記後，始得輸入，以防止不適於國內栽培之新品種引進，產生流弊，甚而影響我國之品種。另爲防止病蟲害侵入或種苗過量輸出入而影響本國種苗事業之發展，並授權中央主管機關於必要時，得限制或禁止種苗之輸出入。（第三十七條、第三十八條）。

㈤訂定罰則：爲貫徹本法之實施，對各種違反行爲，依其情節輕重，分訂刑罰及行政罰之處罰標準，以收儆戒之效。(第四十一條至四十五條)。

㈥外國人及團體之訴權：基於平等互惠原則，凡以同等待遇受理中華民國人或團體申請新品種命名登記或權利登記之外國，我國亦同等待遇賦與該國人或團體，並給予告訴或自訴之權利，以保護其權益。（第四十六條）。

園藝作物育種講習會專刊　423～427(1990)

綜　合　討　論

劉樂州先生(問)

1.本人從事西瓜抗蔓割病育種多年，都沒有很好的突破，此次參加講習會後，對今後西瓜育種，比較有實際及正確的方向。

2.全省種苗業者很多，希望農政單位能經常舉辦講習會幫助業者吸收新知識，以提昇農業層次及進展。

余增廷先生(答)

1.西瓜抗蔓割病是數量性狀，受多對因子所影響，必需用很强的選擇方式，例如選拔的病圃等等，經過多世代的累積，才有一點點的抗病能力，但抗病性似不明顯。野生種的抗耐病品種，大部份植株都很大，若要育成小植株丶小果丶品質好的品種，就會失去原來的抗病性。

2.台灣農業政策發展，以往均以農藝作物爲主，尤其是糧食作物。近來，由於經濟發展，農業型態的改變，園藝作物日漸重視，今後，農試所除舉行通盤性的講習會外，將透過各農改場或推廣中心舉辦有關果樹丶蔬菜或花卉等講習會，經費方面應不成問題，最重要的是參加學員的學習熱心程度。

吳玉珍小姐(問)

1.親本可否申請命名而獲得保護？

2.倘若親本遭受盜用，政府應如何裁定？

余增廷先生(答)

1.種苗法有規定性狀的敘述，假如用親本當做單一自交系來申請專利，其性狀必需詳細敘述，萬一有重複，對方必須提出可靠的來源證明，及其他詳細的性狀記錄資料，以供判別是否爲同一來源，假如無法提供這些資料，就有盜用之嫌。一般親本申請命名，可視爲自交品種，其命名方式亦同。

2.種苗法的立法原則很好，但執行起來很困難。在國際上，種苗法等於是君子協定，歐美日等先進國家對種苗的品牌及形象都很重視，一般種苗公司都在努力建立自己的品牌及聲譽，甚少盜用別人的材料。種苗公司若以親本來申請命名，依種苗法的規定，只能當作自交品種來處理。親本若被別人利用，作爲育種材料是可以的，因經過分離或雜交以後，所育出來的品種，一定與原來的不一樣，因此親本是不受到種苗法的保護。一般種苗公司都不願意拿親本出來申請命名。

陳世賢先生(補充)

種苗公司最好不要拿親本來申請專利，倘若以親本申請專利，政府機關在職務上會給予保密。

莊耿彰先生(問)

1.公家機關經常直接拿國外品種，經馴化後直接推廣，這算不算侵犯對方專利權？

2.種苗商直接引進新品種，並依法取得命名登記，以後若有人要這個新品種，是否需經過該種苗商同意後才可利用？

陳世賢先生(答)

1.在無申請專利保護的情形下，僅是少量的進口用來做爲品種的馴化，經馴化後，選出新的品種來利用推廣，這不算侵犯到對方的專利權。

2.這應視種苗商在台灣是否已取得專利，若只是申請命名登記，則任何人均可進口，任何人均可販賣。

劉樂州先生(問)

一般研究機構之研究人員層次較高，課程安排應著重於比較理論和專門知識方面；而種苗業者則較重視實際面臨的問題。建議今後舉辦講習會時，可按程度和需要分組，盡量採用小班制，以利學員在實習時，有機會親自操作。

余增廷先生(答)

這次講習會，主要是給各位有一些育種觀念，今後會針對果樹、蔬菜、花卉等分組舉行，並且將時間縮短，配合專門技術，實際需要來選擇某一特點，並配合某一地區的特色來舉辦小型講習會。

蔡易新先生(問)

國內公家機構在育種工作，種源收集方面均較私人種苗商廣，投入年限，經費也多，但研究成果，到目前爲止仍是個封閉的形態。希望上級重視研究成果，有效地將這些成果轉移給民間業者，以提昇農業產業。

余增廷先生(答)

政府機關育種研究工作與私人種苗公司育種工作之合作問題，廳長及農委會的主管已有初步構想，希望由政府機關來做。1.種源的收集和保存，2.對私人種苗業者比較困難的育種工作。至於育種的目標並不是在完成品種，而是供給一個差不多可以利用的材料。也就是說政府機關不必去育成一個雜交品種，而只是選育出一些具有抗病性、抗蟲性、耐熱、耐寒、豐產、品質優良的自交系，就可以提供私人種苗業者作爲雜交親本，以育出一個雜交品種，這樣的分工合作，雙方各蒙其利，因爲一個品種育成後，必須經過栽培試驗、推廣、銷售等工作。這些工作若由政府機關來做，似乎有困難，交由私人種苗公司來做，比較方便。但政府機關育種人員是不是不完成品種就沒有工作做？這也不然，因政府機關育種人員要做的事情很多，譬如說比較困難的育種工作，如蔓割病的問題，就需要花很多人力、物力。至於只育成自交系不完成品種，是不是就沒有獎勵，這是不會的，因政府會擬定另一套獎勵辦法，當然也希望種苗公司利用這些育種材料，也要

給這些育種人員一些榮譽，最起碼要說明，親本的來源及育成者的姓名，這也算是給他有一種成就感。

蕭吉雄先生(補充)

在國外某一大學教授提供給某一家種子公司育種材料，如經育成商業品種時，該公司在種子目錄上會註明親本提供者的姓名，這對育種人員也算是一種獎勵。

黃泮宮先生(問)

在目前法規限制下，提供材料給私人公司，會不會有圖利他人的嫌疑？應如何提供，是否已擬出一套辦法？

余增廷先生(答)

不久以前，在農林廳的擴大主管會報裡，曾經討論過這個問題。政府機關育成的材料，交給私人種苗業者，應採取何種方法？是公開招標、拍賣、平均分配還是專利等等，正在研究草擬。

何美惠小姐(問)

1.講習會的講義是否可提供種苗業者參考？
2.如何得知政府公告有關種苗事宜等消息？透過那些管道，可以獲得有關農業的最新資訊？

余增廷先生(答)

1.講習會結束後，農試所會編印成專刊，分送給各學員。
2.很多有關農業的資訊都是免費提送，種苗業者有心收集，可透過各改良場所及農會以獲得。另外有關政府公告種苗法規，可由省府公報、種苗協會或種苗學會得知。

陳世賢先生(補充)

農委會正在積極輔導中華種苗學會和中國種苗協會兩個機購，以利提供種苗業者各項種苗資訊。中華種苗學會將于明年開始出版種苗特刊，會把最新的種苗資訊通知所有會員，業者參加學會就可以很快的獲得這些資訊。中國種苗協會最近協助農委會，與農試所共同策劃編印「台灣地區現有作物名錄--蔬菜篇」之葫蘆科品種特性調查工作，以便種苗法實施後，瓜類品種申請專利之用。會裡希望這兩個機構的業務運轉正常，今後能將有關種苗的資訊，如市場的需求、政府的法令和最新的科技等提供給各業者。

蔡易新先生(問)

種苗法第十九條裡，規定申請種苗專利期間爲十五年，如果全部的作物都是十五年，可能會使大部份從事育種工作人員偏向短期作物育種，這樣會影響研究發展的方向，是否可依作物種類，世代或時間來定專利年限？

陳世賢先生(答)

當初立法爲了方便，所以一律定爲十五年，以個人的立場而言，是希望能分開來定，如營養繁殖作物盡量長一些。目前法令暫定下來，在這法令尙未實施前，是不可以修改的，等到實施一段時間後才可修改，多年生植物如木本植物會定長一些，而草本植物會定短一些，另外有兩股力量也會要求我們改進，一是來自美國對中華民國的智慧財產權的要求，目前著重於著作權上，事實上，中華民國的智慧財產權談判內，植物種苗也是列入智慧財產權內的一項，將來美國也會要求植物種苗的智慧財產權較對美國業者有利的要求，所以國外的壓力會影響我們專利年限的長短。另外在新品種保護聯盟，對年限也有分別，而且世界的趨勢也是這樣，如歐洲對馬鈴薯或多年生植物的專利年限爲25或30年，當然這是需要繳年費才有用，對多年生植物的專利期限比較長，專利期限愈長，對育種人員的獎勵就愈大，所以未來我們一定會朝這方向走。

余增廷先生(補充)

植物專利年限很難界定，因爲科技的突破，有些多年生木本植物利用無性繁殖反而會更快，法令要定得很詳盡，定得恰恰好是很困難的。當初在定法規時也有考慮到這些因素，等法令實施後，實行細則需要修定時，到那時候才來修訂。目前這些長期作物育種工作做得很少，將來需要時，可以針對那時候的情況來修訂。

許淼淼小姐(問)

政府機關育成的新品種，往往因推廣、銷售管道不佳，而未能提供農民使用，甚爲遺憾；可否將新品種交由私人種苗業者代爲銷售？

余增廷先生(答)

政府機關育成一個品種要推廣困難重重，如育成一個新品種經命名後，將來的試作示範、推廣、推銷等程序必須花很多人力、物力的配合。這方面對政府機關來說是相當吃力的工作，有時候即使是一個很好的品種，也會因推廣不佳而被冷漠，如果能與私人種苗商配合，而私人公司也能夠給予育種者一點成就與認可，這樣育種工作就可以做到事半功倍的效果。

杜金池先生(答)

政府機關以前花費很大的力量與經費，育成很好的品種，如鳳山小白菜 1 號、台南甜瓜 8 號等等，均因推廣、銷售道管不佳，農民未能普遍採用。所以將來政府機關育種方向應朝向育成一個中間品種爲主，如育成一個抗病或耐熱的品系，以提供種苗業者利用，這樣政府照顧農民的目標也達成了。

王水車先生(問)

全省種苗業者分散各地，業務上要連絡較爲困難，希望政府能編輯一本有關種苗業者名冊，以利事務上推廣。

余增廷先生(答)

這是民間業者要自我檢討的地方，據農政單位調查的結果，有登記的種苗商與無登記的種苗商相差很多，有很多種苗業者都不來登記，若種苗業者都不登記，政府如何造名冊？如何指導？如何管理？若大家都願意登記，造名冊應是件很簡單的事。目前的中國種苗協學或中華種苗學會就有聯誼的性質，假如種苗業者都能參加這個組織，在名冊上都會有你們的名字；若種苗業者都不參加，即使與他聯絡，也是沒有用的，所以這是要靠種苗業者互相配合的地方。

陳世賢先生(答)

農林廳種子檢查室在77年12月底調查本省種苗業者名錄，包括台北市和高雄市僅有 1 仟多家種苗商登記。事實上本省從事種苗業者不只這個數目，沒有名單無從調查，無法造冊。

林學詩先生(問)

1、園藝作物種類甚多，各場所應如何劃分育種作物？

2、種源庫所收集的材料，是否可提供各改良場所作爲育種上利用？

余增廷先生(答)

原則上是希望各場所間互相合作，另外如指定作物或研究重點指示是有原則性的。如針對地區性的需求，改良場可反應出來；若針對某地區的特殊需要，農委會或農林廳或評議委員會都會另與指示，譬如雜糧作物高粱正面臨這個問題，目前台中 5 號高粱，因採種非常困難，農委會和農林廳就希望指定台中和台南改良場來共同解決這問題。將來種源庫也是會朝向這個合作的目標來做，任何場所有需要種源庫的材料，種源庫是絕對可提供給予利用。

蕭吉雄先生(補充)

在舉辦作物育種計畫研討會時，廳長指示將來育種計畫應由場所來研提，因目前大家所提出的育種計畫很零亂，有些不太重要的作物也提出育種計畫。另外本人覺得育種本身是團隊的工作，需要各方面人才來互相配合，希望上級能同意由不同場所人員共同合作，這樣比較能解決問題。

潘文祥先生(補充)

目前台灣農藝作物方面做得非常成功，這是各個場所互相配合的成果，例如水稻育成一個新品種，很快就可以傳達到各改良場，但是園藝作物方面，除了比較重要的作物如馬鈴薯、柑桔類稍有合作外，其他作物就很少有合作了，從育種到品種的育成至推廣是整體的工作，目前做得不好，主要的徵結是沒有團隊的系列。在果樹方面，產期調節做得非常成功，因爲他們有個團隊在做，在蔬菜方面則非常缺乏這種合作，不單育種工作須要團隊，其他如生理方面也是需要團隊來合作。

園藝作物育種講習會講師名錄

姓名	職務	服務單位	地址	電話
余增廷	省府顧問	台灣省政府	南投市中興新村省府路	07-3821370
謀靜吾	技正	行政院農業委員會	台北市南海路37號	02-3812991
陳世賢	技正	行政院農業委員會	台北市南海路37號	02-3812991
何偉眞	組長	台灣省政府秘書處	南投市中興新村省府路	049-332540
杜金池	所長	台灣省農業試驗所	台中縣霧峰鄉中正路189號	04-3302842
洪立	教授	國立台灣大學園藝系	台北市羅斯福路四段1號	02-3630231
許圳塗	教授	國立台灣大學園藝系	台北市羅斯福路四段1號	02-3630231
黃懿秦	主任	國立台灣大學農藝系	台北市羅斯福路四段1號	02-3630231
胡凱康	副教授	國立台灣大學農藝系	台北市羅斯福路四段1號	02-3630231
李成章	院長	國立中興大學農學院	台中市國光路250號	04-2873181
黃敏展	主任	國立中興大學園藝系	台中市國光路250號	04-2840341
曾夢蛟	副教授	國立中興大學園藝系	台中市國光路250號	04-2840451
俄畢納	主任	亞洲蔬菜研究發展中心	台南縣善化鎮益民寮60號	06-5837801
松達	專家	亞洲蔬菜研究發展中心	台南縣善化鎮益民寮60號	06-5837801
鄭崇成	專家	亞洲蔬菜研究發展中心	台南縣善化鎮益民寮60號	06-5837801
陳正次	副研究員	亞洲蔬菜研究發展中心	台南縣善化鎮益民寮60號	06-5837801
黃永光	副研究員	亞洲蔬菜研究發展中心	台南縣善化鎮益民寮60號	06-5837801
陳文輝	主任	台灣糖業研究所	台南市生產路54號	06-2671911
蕭吉雄	主任	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3399544
沈再發	分所長	鳳山熱帶園藝試驗分所	鳳山市文山路園藝巷四號	07-7310191
盧煌勝	主任	台灣省農業試驗所農藝系	台中縣霧峰鄉中正路189號	04-3302806
曹幸之	研究員	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
林瑞松	副研究員	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
陳炳輝	副研究員	台灣省農業試驗所應動系	台中縣霧峰鄉中正路189號	04-3302301
呂秀英	副研究員	台灣省農業試驗所農藝系	台中縣霧峰鄉中正路189號	04-3302301
徐信次	主任	嘉義農業試驗分所園藝系	嘉義市民權路2號	05-2771340
顏昌瑞	副研究員	嘉義農業試驗分所園藝系	嘉義市民權路2號	05-2771341
鐘維榮	技士	台中區農業改良場	彰化縣大村鄉茄冬路一段36巷200號	04-8523101
楊偉正	助研員	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
張有明	助研員	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
溫英杰	助研員	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
許憲展	助理	台灣省農業試驗所園藝系	台中縣霧峰鄉中正路189號	04-3302301
許家言	助理	台灣省農業試驗所農藝系	台中縣霧峰鄉中正路189號	04-3302301
余志儒	助理	台灣省農業試驗所應動系	台中縣霧峰鄉中正路189號	04-3302301

園藝作物育種講習會學員名錄

姓　名	姓別	服　務　機　關	通　訊　地　址	電　　話
宋　妤	女	國立中興大學園藝系	台中市國立中興大學園藝系	04-2861763
劉孔生	男	國立宜蘭農工專科學校	宜蘭市擺厘號21巷4弄22號	039-352826
黃嘉澤	男	國立宜蘭農工專科學校	宜蘭市農權路三段99巷21號	039-324440
黃光亮	男	國立嘉義農專園藝科	嘉義市嘉農新村30號4樓	05-2248078
葉大振	男	國立屏東農專園藝科	屏東市香揚巷1～115號	08-7228374
凌千里	男	台灣省農業試驗所	台中縣霧峰鄉中正路146巷59弄21號	04-3336034
莊耿彰	男	台灣省農業試驗所	台北市哈密街27號之4	02-5929402
許淼淼	女	農業試驗所鳳山分所	高雄市三民區松江街25號9樓	07-3112793
張麗華	女	農業試驗所鳳山分所	屏東縣潮州鎮南京路121號	08-7889771
林純瑛	女	農業試驗所鳳山分所	高雄縣鳳山市文山里園藝巷4號	07-7310191
利幸貞	女	農業試驗所嘉義分所	嘉義市民權路2號	05-2770320
張哲瑋	男	農業試驗所嘉義分所	嘉義市民權路2號	05-2771341
黃泮宮	男	農林廳種苗改良繁殖場	台中市東山路一段192巷25弄19號	04-2348695
蔡文仁	男	農林廳種苗改良繁殖場	台中縣新社鄉中和街686之15號	045-819549
呂美麗	女	桃園區農業改良場	桃園市民族路163號	03-3322814
邱輝龍	男	桃園區農業改良場	台北縣新店市寶興路60巷32號4樓	02-9144716
楊宏瑛	女	桃園區農業改良場	台中市光復路138號	04-2244506
古錦文	男	台中區農業改良場	台中市南屯區萬和路二段36～6號	04-3893260
潘文祥	男	台南區農業改良場	嘉義市湖內里25鄰湖子內2059號	05-2355552
王仕賢	男	台南區農業改良場	雲林縣斗六市太平路190號	055-327172
林學詩	男	花蓮區農業改良場	花蓮縣吉安鄉吉安村147之7號	038-532935
陸集珊	男	花蓮區農業改良場	花蓮縣吉安鄉吉安村147之8號	038-534702
陳鴻彬	男	台東區農業改良場	嘉義市王田里大同新村76號	05-2763779
陳進分	男	台東區農業改良場	彰化縣員林鎮育英路96之3號	048-329015
楊文振	男	高雄區農業改良場	屏東市公義街24～1號	08-7362827
戴順發	男	高雄區農業改良場	屏東縣萬丹鄉寶厝村36號	08-7773169
沈商嶽	男	高雄區農業改良場	屏東縣內埔鄉大新村大新路530號	08-7700909
李國榮	男	金門縣農業試驗所	金門金湖鎮小徑18號	金門 33292
楊慧明	女	金門縣農業試驗所	金門金城民權路121號	金門 29896
邱國偉	男	博友貿易股份有限公司	高雄市本館路601巷13號	08-3813881
王水車	男	勝利農藥種子行	彰化縣秀水鄉福安村中興巷8號	047-692226
何美惠	女	第一種苗股份有限公司	嘉義市博愛路2段284之18號	05-2375012
黃克昌	男	新金鐘種苗有限公司	台南市建平8街439號	06-2200382
邱泰碩	男	大三種子有限公司	高雄市七賢二路65號9樓3室	07-2113101
鍾玉珍	女	大三種子有限公司	高雄縣旗山鎮福正街32之1號	07-6692032
蔡易新	男	鮮美農產有限公司	彰化縣溪湖鎮長青街20巷14號	048-853855
何泰然	男	生生種子公司	台南市健康路133巷77之1號	06-2612353
謝炯明	男	生生種子公司	台南市東榮街115巷19號	06-2376458
駱宏順	男	台灣農產企業公司	台北市吳興街50巷12弄4號2樓	02-7382681
吳玉珍	女	農友種苗公司	高雄縣仁武鄉考潭村新興巷330號	07-3719725
王振昌	男	農興貿易有限公司	台中縣豐原市中正路432號	045-268533
李秀眞	女	農興貿易有限公司	台中縣豐原市西安街155號	045-245096
劉樂州	男	國寶農園	雲林縣虎尾鎮平和里青埔2～3號	056-323065

園藝作物育種講習會上課時間表

第一階段：自10月16日到10月24日

10月16日星期一		
08:10～08:40	報　到	
08:50～09:20	開班典禮	杜所長金池
09:30～12:00	園藝作物育種之方法	洪　立博士
13:50～17:10	園藝作物育種之方法	洪　立博士
10月17日星期二		
08:10～09:00	電腦在育種上之利用	胡凱康博士
09:10～12:00	數量遺傳在育種上之應用	胡凱康博士
14:10～17:00	全互交與組合力在育種上之應用	李成章博士
10月18日星期三		
08:30～11:20	作物基因型與環境交感	呂秀英博士
14:10～17:00	蔬菜作物之族群改良實例	盧煌勝博士
10月19日星期四		
08:30～11:20	移位因子、遺傳變異與作物改良	黃懿秦博士
14:10～17:00	溫度逆境生理在園藝育種上之應用	曾夢蛟博士
10月20日星期五		
08:30～11:20	園藝作物之雜種優勢及其利用	李成章博士
14:10～17:00	實習：除雄、授粉、雄不孕、蕾期授粉螢光顯微鏡觀察	曹幸之博士 楊偉正先生
10月21日星期六		
08:30～11:20	園藝作物抗病育種之理論及實際	蕭吉雄博士
14:10～17:00	休　息	
10月22日星期日	休　息	
10月23日星期一		
08:30～11:20	生物技術在園藝作物改良上之應用	許圳塗博士
14:10～17:00	實習：電泳技術、人工種子合成、DNA 分離等	許圳塗博士 張有明先生

10月24日星期二

08:30～11:20	園藝作物抗蟲育種	陳炳輝博士
14:10～17:00	實習：昆蟲之認識、養蟲方法、接種、及抗蟲性評估	陳炳輝博士 余志儒先生

第二階段：自11月6日到11月11日

11月6日星期一

08:10～10:00	組織培養在園藝育種上之應用	陳文輝博士
10:10～12:00	植物組織培養在作物育種上的應用	何偉眞博士
14:10～17:00	實習：胚培養、花藥培養、細胞培養、原生質體培養等	許家言小姐 溫英杰先生

11月7日星期二

08:30～11:20	花卉育種概論	黃敏展博士
14:10～17:00	實習：生長點培養、無菌播種	林瑞松博士 許憲展先生

11月8日星期三

08:10～12:00	茄科蔬菜育種	俄畢納博士 陳正次先生
14:10～17:00	十字花科蔬菜育種	沈再發所長

11月9日星期四

08:10～12:00	豆科蔬菜育種	松　達博士 鍾維榮先生
14:10～17:00	瓜類蔬菜育種	蕭吉雄博士

11月10日星期五

08:10～10:00	果樹育種概論	徐信次主任
10:10～12:00	果樹育種策略及台灣果樹育種常見之問題	顏昌瑞博士
14:10～17:00	作物遺傳資源的保存及其利用－概念與應用	鄭崇成博士 黃永光先生

11月11日星期六

08:10～10:00	植物種苗法介紹	陳世賢先生
10:10～12:00	綜合討論	杜所長金池、余顧問增廷 諶技正靜吾、蕭主任吉雄